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Fisheries biology, ecology and recreational harvesting of ghost shrimp (trypaea australiensis) in south-eastern Australia

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Fisheries biology, ecology and recreational harvesting of ghost shrimp (*Trypaea australiensis*) in south-eastern Australia

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"Doing what little one can to increase the general stock of knowledge is as respectable an object of life, as one can in any likelihood pursue"

Charles Darwin

Dedicated to my wife Leanne and son Lachlan,

for the precious time lost.

&

To my parents, David and Judith Rotherham

for a lifetime of support, encouragement and inspiration.

Thesis Declaration

I, Douglas Rotherham, declare that this thesis, submitted in partial fulfilment of the requirements for the award of Doctor of Philosophy, in the School of Earth and Environment Sciences, University of Wollongong, is wholly my own work unless otherwise referenced or acknowledged. The document has not been submitted for qualifications at any other academic institution.

Douglas Rotherham

31 August 2004

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ABSTRACT

Burrowing ghost shrimp, *Trypaea australiensis* Dana 1852*,* are a popular bait organism harvested from estuarine intertidal sediments in eastern Australia by recreational and commercial fishers. Previous investigations concerning the biology and ecology of this species have been limited in this region, particularly for south-eastern Australia. Despite considerable public concern about the species, catches of *T. australiensis* are largely unregulated, at least partly because there has been virtually no data to support the development of appropriate management strategies. The present research was initiated to address the lack of baseline data on the fisheries biology, ecology and recreational harvesting of *T. australiensis*, to assist in providing a more sustainable approach to management and conservation.

Preliminary studies comparing different quantitative sampling methods demonstrated that manual suction pumps (i.e., yabby pumps) were a more efficient and representative method of sampling *T. australiensis* than coring devices. Following the determination of a suitable sampling methodology, a hierarchical sampling program was established in south-eastern Australia to investigate spatial and temporal patterns of abundance, reproduction and growth. This involved sampling three estuaries spanning 300 km of coastline, namely Port Hacking, Shoalhaven River and Moruya River. The experimental design incorporated nested spatial scales ranging from hundreds of kilometres (between estuaries), kilometres (between sites), tens to hundreds of metres (between plots) and metres (between quadrats). Sampling was conducted over a two-year period, monthly for the first year and quarterly for the second. One site was sampled monthly for the entire study period to investigate differences between years.

Overall, abundances were more variable on smaller spatial scales between sites within estuaries and between plots within sites. However, it was evident that these spatial patterns also changed through time. Increases in abundance across all sites during spring/summer periods, resulted in an increased patchiness in abundance within sandflats at a scale of tens to hundreds of metres (between plots), and less patchiness at the smallest spatial scales of metres (between replicates). This result suggested that increases in abundance might be explained by a redistribution of animals due to spawning aggregations, rather than nett increases in shrimp numbers. Furthermore, while recruitment occurred during spring and summer months, increases in numbers and biomass during these periods were greater than would be expected from recruitment alone. Increases in temperature and salinity may have initiated hypothesized breeding aggregations, although relationships between environmental variables and abundance were not significant even though general trends were evident.

Timing of recruitment was consistent between years and included a latitudinal pattern of earlier recruitment in southern estuaries, which was probably related to earlier breeding periods at these locations. Despite this, the supply of new recruits was consistent over large geographic scales and patchy within and between sites within estuaries, suggesting distribution and survival of larvae may be influenced by local hydrology and environmental conditions. Stronger recruitment in consecutive years may have been related to prevailing drought conditions, enhancing survival of larvae due to consistently higher salinities resulting from reduced freshwater inputs.

Relationships between number of burrows and abundance of *T. australiensis* were investigated, since burrow counts are often used to estimate densities of ghost shrimp. Some significant relationships were observed between number of burrows and abundance of *T. australiensis*. However, spatial and temporal inconsistencies indicated that counting of burrow openings was not always a reliable predictor of relative abundance. Estimates of the magnitude of populations suggested that standing stocks of *T. australiensis* at individual sites were in the order of millions of individuals.

Sex ratios were significantly biased towards females following sexual maturity and this pattern was spatially and temporally consistent at all locations. Hypotheses explaining female-biased sex ratios remain speculative for *T. australiensis* and other thalassinids and further research is required. Despite consistencies related to female-biased sex ratios, there was considerable intra-specific variability in the reproductive biology of *T. australiensis* over different spatial and temporal scales. Female size at maturity, based on ovigerous females, was smaller for populations in southern estuaries. However, the specific roles of environmental and/or density-dependent factors such as population abundance, temperature and availability of food in determining these patterns are unclear. Similarly, these factors may also influence commencement of breeding seasons, which was asynchronous and occurred progressively earlier in southern populations.

Unimodal breeding seasons generally lasted 5 to 6 months, with ovigerous females occurring from mid-summer through to autumn across most sites.

Fecundity increased linearly with female size across all sites and decreased with increasing latitude. Estimates of reproductive output also indicated that fecundity was higher for females carrying late stage embryos, compared to freshly extruded eggs, which suggested that studies counting only uneyed embryos may underestimate fecundity. Measurements of embryos indicated that *T. australiensis* employs a strategy of high fecundity and small egg size relative to other thalassinids. Number of broods per female was not experimentally determined, although theoretical maximums of between 3 and 5 broods per season were estimated.

Differences in patterns of relative growth between males and females explain sexual dimorphism in size and shape of primary chelae. Males also appeared to undergo a puberty moult at smaller sizes than females. The enlarged cheliped of male *T. australiensis* and other ghost shrimp is generally believed to be used in competitive interactions with other males, although more research is required to validate this hypothesis. Size at maturity as determined from analyses of relative growth was significantly related to latitude, with males and females from southern estuaries maturing at smaller sizes. However, estimates of female size at maturity from relative growth analyses did not compare well to sizes of ovigerous females, suggesting that the puberty moult may not coincide with gonad development. Future studies should attempt to determine male size at maturity based on reproductive condition rather than relying on analyses of relative growth data.

Length frequency analyses indicated that *T. australiensis* is a fast growing species with a life-span of 3 to 4 years. Results suggesting a longer life-span at some sites

are likely to be an artefact of the ELEFAN procedure. There were no consistent geographic trends in growth parameters, although lower growth rates and asymptotic lengths at sites in the Moruya River, probably reflect the smaller size of individuals in this estuary. Patterns of fishing mortality and exploitation ratios determined from stock assessment procedures suggest that populations across all sites are either currently under-exploited or approaching optimal harvesting rates. However, theses results are of a preliminary nature, given questions regarding the reliability of ELEFAN for some data sets.

Recreational creel surveys at three locations (Maianbar, Shoalhaven Heads and Garlandtown) demonstrated that individual anglers frequently harvested large numbers (> 200) of *T. australiensis* during single fishing trips. There were no differences in mean harvesting time between locations, with differences in CPUE therefore reflecting fishing quality. Boat-based anglers spent significantly less time harvesting than shore-based anglers. High rates of refusal to either participate in the survey, or allow catches to be handled, were consistent with other studies of *T. australiensis* in Australia and are related to time constraints and fragility of the organism. Anglers commonly underestimated number of shrimp harvested and over-estimated time spent harvesting, which has consequences for studies that rely on data from telephone surveys or diaries. Anglers removed large numbers of *T. australiensis* from individual locations during single low-tide periods. For example at the Maianbar site, mean estimated catch during a 6-hour low-tide event occurring on a summer weekend/holiday day, was over 4,500 individuals. Although total estimated harvests were considerable during the 6-month study period, recreational catches represented fewer than 2% of estimated stock sizes

across all sites. A doubling of these estimates for an entire year was considered an overestimate of annual harvest, given that most angers claimed they did not harvest during winter months.

The results of this research have been discussed in relation to the life-history of *T. australiensis* in south-eastern Australia, the harvesting of the species, the objectives of sustainable management of populations and scope for further research. Specifically, restrictive management is not advocated for *T. australiensis* in NSW. However, continued monitoring and research is necessary to determine the long-term ecological impacts of harvesting activities on populations, communities and habitats, as well as experimental tests of hypotheses constructed to explain observed patterns.

Chapter 1

Introduction

1.1 General background

There is a long history of harvesting organisms from coastal environments, dating back to prehistoric times when invertebrates such as bivalve molluscs provided important sources of food (Voigt, 1973; Volman, 1978; Avery and Siegfried, 1980; Beaton, 1985; Richards and Hedges, 1999). In many regions of the world, the harvesting of fish products from intertidal areas by indigenous and coastal populations has changed little, and these populations still support subsistence and artisinal fisheries (Jerardino *et al.*, 1992; Lasiak, 1992; Pedersen *et al.*, 2003). In many developed countries, harvesting from marine shorelines has been conducted on a commercial scale for much of the last century (Brown, 1993; Murray-Jones and Steffe, 2000). An emergent trend in recent decades has involved collection of marine biota for a wide range of recreational purposes, including fisheries for food and bait (Kingsford *et al.*, 1991; Wynberg and Branch, 1991; Underwood, 1993a; McLachlan *et al.*, 1996; Murray-Jones and Steffe, 2000).

Despite the historical context of anthropogenic harvesting within intertidal ecosystems, the impacts of human predation on populations and communities have only been addressed in the last 20 years (Eeekhout *et al.*, 1992; Moreno, 2001). The effects of subsistence harvesting have been well documented during this time, particularly for some rocky shores in Chile and South Africa (see review and references cited in Moreno, 2001). Similarly, the impacts of commercial harvesting activities on intertidal soft-sediment faunas has received considerable

attention (Peterson *et al.*, 1987; Olive, 1993; Beukema, 1995; Spencer *et al.*, 1998; Ferns *et al.*, 2000; Kaiser *et al.*, 2001). By comparison, the total number of studies that have considered the direct and indirect effects of recreational harvesting on marine shoreline invertebrates and ecosystems are relatively few (Blake, 1979; Jackson and James, 1979; McLusky *et al.*, 1983; Cryer *et al.*, 1987; Keough *et al.*, 1993; Sharpe and Keough, 1998). In fact, for many harvested species, basic biological information on life-history (growth, reproduction, abundance, recruitment) and population dynamics, which are fundamental to stock assessment and sustainable management, are lacking. Management is further confounded by public and political perceptions that recreational fishing is less destructive than the activities of commercial fishers (Kearney, 1999, 2001; McPhee *et al.*, 2002). Although, in recent times there has been a growing realisation that the recreational catch of particular species of finfish exceeds that of the commercial sector (West and Gordon, 1994; Kearney, 1995; McPhee *et al.*, 2002). Nevertheless, characteristics of the catch and effort for many important recreational invertebrate fisheries remain unknown and lead to questions about ecological sustainability of these species.

In south-eastern Australia, previous studies of recreational harvesting and biological and ecological studies of target organisms have largely been restricted to rocky shores (Fairweather, 1991; Kingsford *et al.*, 1991; Underwood, 1993a). Indeed, the biology and ecology of soft-sediment fauna is poorly studied in this region compared to other coastal habitats (but see Morrisey *et al.*, 1992a; Morrisey *et al.*, 1992b; James and Fairweather, 1996). Given the cryptic nature of soft-sediment fauna, where individuals are buried or actively burrow within the

substratum, representative sampling is often difficult and labour intensive. Currently, recreational harvesting of rocky shoreline plants and animals and the protection of biodiversity are managed by a series of Marine Protected Areas (MPA's) and marine reserves, as well as bag and size limits in New South Wales (NSW) (Anon, 2004d). However, despite containing some of the most commonly harvested organisms, estuarine environments in NSW such as intertidal sand and mud flats and their associated fauna, are generally not afforded the same level of protection as rocky shores. For some of the key species, recreational harvesting is almost completely unrestricted in terms of access to the fishery, participation, bag and size limits and collection of reproductive females. This situation is at least partly due to an absence of scientific data needed for assessment and management. The present study addressed the shortfall in information for one popular bait organism harvested in south-east Australian estuaries, the ghost shrimp *Trypaea australiensis*.

1.2 Statement of the problem

The ghost shrimp, *Trypaea australiensis* (Plate 1.1), is a burrowing marine decapod crustacean, which inhabits intertidal sand/mud flats on the east coast of Australia, from Low Isles in Northern Queensland, to Port Philip Bay in Victoria. Burrows of *T. australiensis* are easily recognised (Plate 1.2), with densities of up to 500 m^{-2} common in some areas (Hailstone and Stephenson, 1961). Animals are extracted from their burrows using a manual suction device known as a 'yabby' pump (Plate 1.3), derived from the common name of *T. australiensis* in QLD and northern NSW. In south-eastern Australia, *T. australiensis* are generally referred to as nippers, since the word 'yabby' also applies to the freshwater crayfish,

Cherax destructor, and causes confusion. Nevertheless, it is widely acknowledged that *T. australiensis* is premium live bait for catching popular recreational fish species such as yellowfin bream (*Acanthropagrus australis*), dusky flathead (*Platycephalus fuscus*) and whiting (*Sillago ciliata*).

Plate 1.1. Male (a) and female (b) *T. australiensis*. Note orange egg mass under abdomen of female and sexual dimorphism of enlarged primary chela.

Plate 1.2. Close-up of burrows of *T. australiensis* during low-tide at Maianbar, Port Hacking, NSW.

Plate 1.3. Photograph demonstrating the use of a yabby pump to harvest *T. australiensis* at Maianbar, Port Hacking, NSW.

A recent national survey of recreational fishers in Australia indicated that *T. australiensis* was the second most harvested species by numbers in NSW, with a catch of about 3 million animals per annum (Henry and Lyle, 2003). Commercial harvesting of *T. australiensis* from within NSW estuaries, is permitted under hand gathering endorsements in the Estuary General Fishery (Anon, 2003). Over the past decade, catches of *T. australiensis* in NSW have averaged approximately 1400 kg per annum (approximately 700,000 animals) (NSW Fisheries, unpublished commercial catch data). However, in recent years catches have dropped dramatically (Fig. 1.1), coinciding with the buy-out of commercial fishing effort in many estuaries in NSW. Indeed, the entire reported commercial catch of *T. australiensis* for the year 2002/2003 was only 16 kg. These figures indicate that *T. australiensis* is now almost exclusively targeted by the recreational fishing sector.

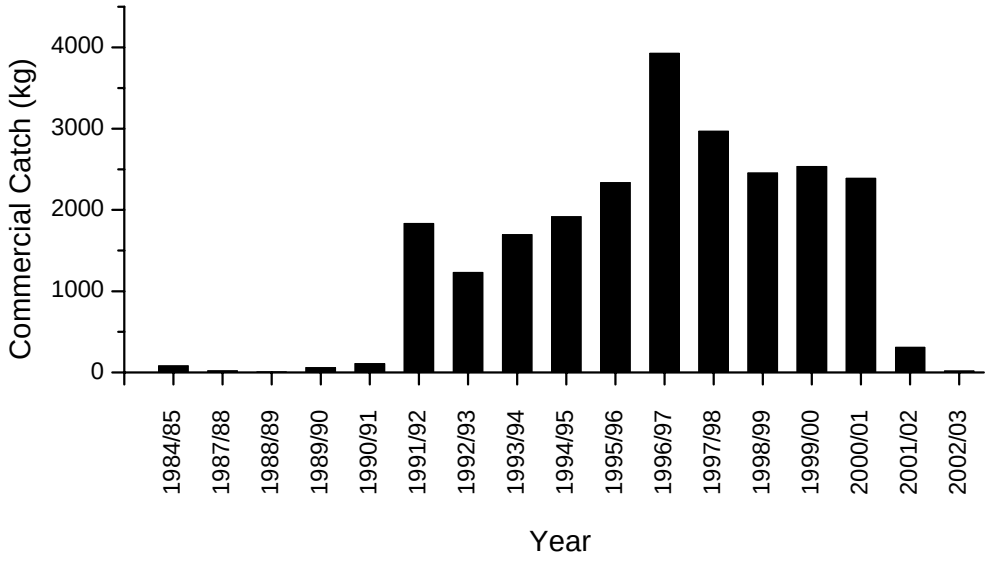


Figure 1.1. Reported commercial catch (kg) of *T. australiensis* from the Estuary General Fishery in NSW, between 1984/85 and 2002/2003 (NSW Fisheries, unpublished commercial catch records).

Despite the reported level of recreational harvesting, there are currently very few restrictions on catching *T. australiensis* in NSW, other than a general fishing licence. Recreational anglers are permitted to collect an unlimited quantity of animals from almost any location and of any size, regardless of reproductive condition. This current low level of management is difficult to justify without information on the population biology, ecology and harvesting of *T. australiensis*. It is widely acknowledged that in unmanaged open-access fisheries, utilisation of target species is often not optimal or sustainable and may result in stock collapse (Hilborn and Walters, 1992; King, 1995; Jennings *et al.*, 2001). The potential for over-harvesting of *T. australiensis* certainly exists, particularly at more accessible locations (Hailstone and Stephenson, 1961). However, assessing the impacts of harvesting and prescribing management strategies requires baseline data on the population biology and ecology of an organism, together with information on recreational catch and effort and patterns of harvesting. A lack of such information has certainly hindered management of *T. australiensis* in NSW.

In the absence of sound scientific data, anecdotal information and the precautionary approach has been used in the management of some of the fisheries resources in NSW (Smith and Pollard, 1996). This has resulted in some other bait organisms such as pipis, beach worms and cockles being protected by size and bag limits prior to any significant scientific assessment. However, for *T. australiensis*, anecdotal information on the status of the resource varies between locations and appears contradictory at best. This situation is undesirable, as *ad-hoc* management decisions may result from scientifically unjustified recommendations of vocal and influential lobby groups. Also, the political will to

frame precautionary conservation measures in the absence of scientific data is often lacking, particularly when the decision is seen to be unpopular across the broader community (Smith and Pollard, 1996). In recognising the need for a more scientific approach towards assessment and management of *T. australiensis*, the following gaps in knowledge were identified.

1.3 Present gaps in knowledge

Very few studies have investigated the population biology and ecology of *T. australiensis* in Australia. In fact, such studies are relatively uncommon for thalassinids worldwide, despite the diversity and ecological significance of the taxa, which has been the focus of other research (see review by Felder, 2001). For example, of the 71 selected studies published between 1990 and 2000 reviewed by Felder (2001), only 15 (21%) directly investigated population and life-history parameters such as abundance, growth, reproduction and recruitment. In contrast the movement of sediment associated with burrowing activities and trophic modes of ghost shrimp (referred to as bioturbation), has been the focus of much research. Consequently, the effects of bioturbating ghost shrimp on the physical and biogeochemical properties of substrata (Koike and Mukai, 1983; Tudhope and Scoffin, 1984; Vaugelas and Buscail, 1990; Ziebis *et al.*, 1996; Rowden *et al.*, 1998; Berkenbusch and Rowden, 1999; Katrak and Bird, 2003) and the structure of associated infaunal communities (Posey, 1986; Branch and Pringle, 1987; Tamaki, 1988; Posey *et al.*, 1991; Dittmann, 1996; Berkenbusch *et al.*, 2000) are comparatively well known.

Much of the available information on aspects of the population dynamics and life-history of *T. australiensis* in eastern Australia comes from studies in Queensland and Victoria, with the biology of the organism virtually unknown in NSW. Previous studies in Australia have either been conducted over limited spatial and temporal scales, are somewhat outdated (e.g., Hailstone and Stephenson, 1961), or have not sampled populations quantitatively. As a result, various aspects of the biology and ecology of *T. australiensis* still require investigation. For example, few studies have documented patterns in distribution and abundance of *T. australiensis* and previous accounts were restricted to single sites and estuaries. Understanding spatial and temporal variation in abundance of an organism across a hierarchy of scales, provides a logical starting point for experiments that explain observed patterns and also a scientific basis for assessment and management of anthropogenic impacts (Andrew and Mapstone, 1987; Levin, 1992; Underwood, 1992; Underwood *et al.*, 2000). One explanation for the lack of quantitative research on the biology and ecology of *T. australiensis* and indeed other ghost shrimp is the difficulty in obtaining adequately representative samples. This highlights the need to establish a sampling methodology for *T. australiensis* that is quantitative, rapid and repeatable.

Although previous studies of *T. australiensis* have often focused on reproductive biology (Hailstone and Stephenson, 1961; Nurse, 1980; Kenway, 1981; McPhee and Skilleter, 2002a) many aspects remain unclear. For example, few studies have investigated size-specific fecundity or embryo size in any detail, and certainly, no comparisons of reproductive biology or potential have been made over a range of spatial and temporal scales. Previous studies in New Zealand have demonstrated

latitudinal variation in the reproductive biology of a related species *Callianassa filholi* (Berkenbusch and Rowden, 2000). Hence, regional differences in the reproductive biology of *T. australiensis* are possibly expected in Australia and it is likely that previous studies in Queensland would be of little utility for stock assessment and management in NSW.

Given that patterns of abundance have not been well documented for *T. australiensis*, it is not surprising that recruitment is also poorly understood. For example, Hailstone and Stephenson (1961) did not quantitatively investigate recruitment, as their sampling methodology did not capture small post-larval individuals. Other studies have provided information on recruitment for narrow geographic ranges or small temporal scales (< 1 year) (Kenway, 1981; McPhee and Skilleter, 2002a). Similarly, studies of growth are limited to single sites and estuaries and there has been no attempt to apply length frequency analyses to estimate growth parameters of *T. australiensis* over a number of spatial and temporal scales. Nor have estimates of growth been obtained through tagging experiments, which could be carried out in the field and laboratory. The small size and fragility of *T. australiensis* makes traditional tagging methods unsuitable. Hence, investigations of suitable alternative tagging methods for studies of growth and other population parameters is another area that requires research.

In addition to knowledge of the population biology and ecology of *T. australiensis*, characteristics of catch and effort and extent of harvesting are required for stock assessment and management. The National Recreational and Indigenous Fishing Survey in Australia, recently published details of harvesting of

T. australiensis in NSW, which related to catch and effort for the entire coastline (Henry and Lyle, 2003). Data on the total annual catch of *T. australiensis* for particular states are provided. However, impacts of harvesting are more likely to be localised, occurring on smaller spatial scales, such as individual sandflat locations within estuaries. Indeed the entire harvest from a particular estuary may come from a single site. Yet there are few published data on how many people actively harvest *T. australiensis*, or how many organisms are taken from individual sites during low-tide periods on any given day. Small-scale creel surveys conducted at a number of locations can provide such data, as well as other information on the characteristics of harvesting including fisher demographics, party size, harvesting patterns, size ranges of catches and retention of ovigerous (egg-carrying) females. The National Recreational and Indigenous Fishing Survey Henry and Lyle, 2003, collected some unpublished information on the harvests of *T. australiensis* in NSW (Gary Henry, pers comm.), and this warranted synthesis and analysis. Furthermore, given that the surveys were conducted using telephone interviews, there is a need to validate the results, through comparisons of field-based observations.

From the gaps in knowledge described above, the aim of this thesis was to gain an understanding of the population biology, ecology and harvesting of *T. australiensis* over a range of obvious spatial and temporal scales, relevant to stock assessment and management of the resource in south-eastern NSW. A number of research objectives were developed within the time frame available and limits on resources.

1.4 Thesis objectives

The primary objectives of this research were to:

1. Develop and compare different quantitative methods of sampling *T. australiensis* and design a robust sampling strategy for investigations of population biology, ecology and life-history in south-eastern Australia.
2. Investigate the population biology and ecology of *T. australiensis* through quantitative studies of spatial and temporal patterns of abundance, reproductive biology and growth over a hierarchy of scales in south-eastern Australia.
3. Investigate characteristics of harvesting of *T. australiensis* in south-eastern Australia through field investigations at selected sites; to analyse existing data from the large-scale National Recreational and Indigenous Fishing Survey (Henry and Lyle, 2003); and to compare results to gain an understanding of the nature and extent of recreational harvesting of *T. australiensis*.
4. Synthesise findings of the research and provide an overview of the life-history and status of *T. australiensis* in south-eastern Australia, and make recommendations for conservation and management and directions for future research.

A further objective was to conduct a preliminary investigation of the utility of several internal tagging methods for *T. australiensis*. As these studies did not warrant a separate chapter in this thesis and results were not critical to studies in subsequent chapters, the results are presented in Appendix 1, in the form of a short journal manuscript.

1.5 Thesis structure

This thesis is composed of seven chapters. A separate review of relevant literature is provided in the introductory section of each chapter.

In Chapter 1, a general background and need for the research has been outlined along with the objectives of the thesis. The remainder of this chapter will provide descriptions of the study region and estuaries sampled, as well as information on the taxonomy of *T. australiensis*.

Chapter 2 is presented in the form of a manuscript (with some minor formatting changes) that has since been published (Rotherham and West, 2003). This has resulted in some overlap of introduction and methods sections with Chapters 1 and 3. As maps of study locations and sites are not included in the manuscript, they have been included elsewhere in the thesis (Chapters 1 and 3). Chapter 2 compares different quantitative methods of sampling *T. australiensis* and outlines an optimal experimental procedure for collecting representative samples. This chapter meets objective 1 (see above).

Chapter 3 describes two studies related to spatial and temporal patterns of abundance of *T. australiensis* in south-eastern Australia. The first study examined patterns of abundance of *T. australiensis* over a hierarchy of spatial scales and investigated changes in spatial patterns over time. This involved sampling two sites within each of three estuaries on a monthly basis for a period of one year and then quarterly for a second year. The second study examined temporal patterns of abundance at a hierarchy of temporal scales (months to years). Sampling was

conducted on a monthly basis at one particular site for a two-year period. This chapter meets the first component of objective 2 and the sampling programs contained within also form the basis for the collection of data on reproduction and growth of *T. australiensis*, which are investigated in subsequent chapters.

Chapter 4 examines intra-specific variability in the reproductive biology of *T. australiensis* across a range of spatial and temporal scales in south-eastern Australia. This includes investigation of sex ratio of populations, female size at maturity, commencement and duration of breeding seasons, fecundity, and egg size. These parameters are important in considerations of management strategies such as size limits, closures, and restrictions on collection of egg-carrying females. Geographic differences are discussed in relation to latitude, local population dynamics and physical environmental conditions. This chapter meets another component of objective 2.

Chapter 5 investigates spatial and temporal variation in relative and absolute growth parameters of *T. australiensis* in south-eastern Australia. Analyses of relative growth parameters are used to determine size at maturity and investigate sexual dimorphism and heterochely. Modelling of absolute growth parameters using electronic length frequency analysis (ELEFAN) are compared within and between widely separated estuaries. Mortality rates are also estimated, allowing assessment of the current level of exploitation. Results are discussed in relation to conservation and management of the species and the suitability of ELEFAN for determining growth parameters of *T. australiensis*. This chapter addresses the final component of objective 2.

In Chapter 6, data are presented on the extent and intensity of small-scale recreational harvesting of *T. australiensis* during spring and summer periods at three selected sites in south-eastern Australia including: catch per unit effort (CPUE), effort and mean daily harvests; characteristics of harvesting (such as fisher demographics, party size and retention of small and ovigerous females); as well as estimates of the total recreational catch for specific periods. Results are discussed in relation to results (both published and unpublished) obtained from the National Recreational and Indigenous Fishing Survey (Henry and Lyle, 2003), and to manipulative experimental procedures, which are required for an ecosystem approach to conservation and management of the species. This chapter meets objective 3.

In Chapter 7, the major findings of the research are presented and synthesised, including an overview of the life-history and status of *T. australiensis* in south-eastern Australia. Recommendations for current and future management of the species are discussed and directions for future research are identified. This chapter meets objective 4.

1.6 Description of the study region

1.6.1 Coastal and geological environment

Studies described in this thesis were undertaken in estuaries of south-eastern Australia between Sydney and Moruya, including Port Hacking, the Shoalhaven River and Moruya River (Fig. 1.2). These estuaries were selected as they contain

accessible estuarine tidal flats, where populations of *T. australiensis* are harvested by recreational anglers for bait.

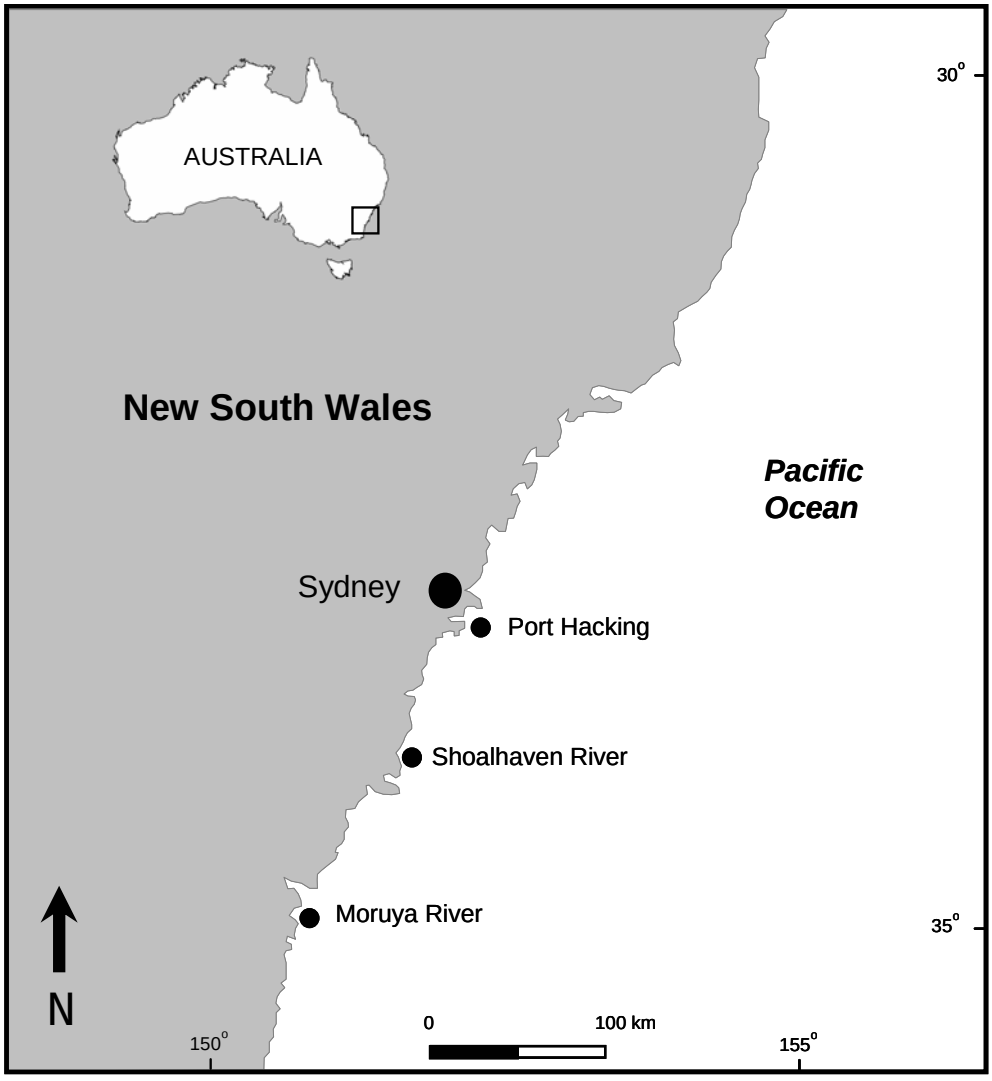


Figure 1.2. Location of estuaries sampled in south-eastern Australia.

Estuaries along the south-eastern Australian coastline were formed during quaternary glacial and interglacial periods by oscillating sea levels, which repeatedly excavated and in filled bedrock valleys (Roy, 1984; Roy *et al.*, 2001). Since the end of the post-glacial marine transgression some 7000 to 8000 years ago, many estuaries in this region have been located landward of deposited sand barriers. These estuaries are now connected to the ocean by dynamic entrances, which may be permanently or intermittently open depending on estuary-mouth hydrodynamics and fluvial input, and conditions may fluctuate between marine and freshwater (Roy, 1984; West *et al.*, 1985). In contrast, open embayments are located seaward of sand deposits and are characterised by marine conditions (Roy, 1984; Roy *et al.*, 2001).

Coastal water bodies in south-eastern Australia have been classified on the basis of their geomorphology into 5 groups (Roy, 1984; Roy *et al.*, 2001) which includes; (1) Bays; (2) Tide dominated estuaries; (3) Wave-dominated estuaries; (4) Intermittent estuaries; (5) Freshwater bodies. These 5 groups are further divided into 13 different types. Classification is also based on the stage of evolutionary development (Roy, 1984; Roy *et al.*, 2001), ranging from mature infilled forms, to relatively youthful forms with very little infilling. Estuaries from groups 2 and 3 are represented in this thesis, the specific types including drowned river valleys (Port Hacking) and mature barrier estuaries (Shoalhaven River and Moruya River). Drowned river valleys are formed in bedrock valleys and characterised by permanently open entrances that form semi-protected bays with a full tidal range and large flood tide deltas composed of shelf sand. Mature-barrier estuaries are often characterised by large rivers that occur behind wave deposited

beach sand, with constricted inlets and smaller tidal ranges than drowned river valleys (Roy *et al.*, 2001).

1.6.2 Climate and oceanography

The climate of the study region is classified as temperate and is characterised by warm summers and mild winters around Sydney, with milder summers and cooler winters towards Moruya. Temperature and rainfall averages based on at least 10 years data (Anon, 2004a) for each estuary are summarised in Table 1.1. Rainfall is dominated by ENSO and other climatic events which may operate on decade-long cycles (Powers *et al.*, 1999).

Mean monthly sea temperatures also change latitudinally along the coast of NSW. In waters off Sydney, sea surface temperatures range from 17.7 - 23.5°C, with a yearly average of 20.6°C (Anon, 2000a). Sea surface temperatures around Moruya are lower and range from 16.3 - 22.7°C, with a yearly average of 19.5°C (Anon, 2000a). Prevailing winds along the south-east Australian coastline are south-westerly to westerly in winter, with south-easterly flows and north-easterly sea breezes dominating in summer (Anon, 2004a).

The East Australian Current (EAC) is a south flowing western boundary current, which dominates oceanographic conditions in south-eastern Australia. Beginning as a surface stream in the Coral Sea, the current moves inshore as it crosses the continental shelf on its run southward (Anon, 2000b). At about 32.5°S, the current heads seawards, forming south-flowing counter clockwise eddies as large as 200 km across, which direct water northwards on the shelf edge. Current velocities

fluctuate within and between regions and range from 2.0 ms^{-1} in northern areas, to 1.0 - 1.5 ms^{-1} in cental and southern parts. The EAC is strongest during summer periods, with flows reducing to half in winter. The distribution of planktotrophic larvae into estuarine environments along with coastal sea surface temperatures are largely controlled by the EAC. Tides in the region are semi-diurnal with a maximum spring range of 2 m.

Table 1.1. Summary of temperature and rainfall data for selected regions in south-eastern Australia based on at least 10 years data (Anon, 2004a).

Location	**Temperature (°C)**				**Rainfall (mm)**	
	summer		winter		summer	winter
	Min	Max	Min	Max		
Port Hacking	18	25	8	17	95	89
Shoalhaven	16	25	7	16	98	78
Moruya	16	24	7	17	89	66

1.6.3 Study locations

Port Hacking

Port Hacking is a drowned river valley located 35 km south of Sydney (Fig. 1.2, Plate 1.3). It has a catchment area of 180 km^2 and an open water area of 11 km^2 (West *et al.*, 1985). Water depth at the permanently open entrance is approximately 12 m. Further upstream, water depth is variable and large tidal flats are exposed in many areas during low-tide periods. The majority of the northern foreshore is high density urban landscape and almost 25 years ago, between 50% and 75% of the shoreline and catchment was in natural condition (Bell and Edwards, 1980). Since then, there has been rapid population growth within the

catchment. Much of the southern foreshore and catchment is within the Royal National Park and Garrawarra State Recreation Area, with small coastal villages at Maianbar and Bundeena. The estuary supports approximately 0.328 km^2 of mangroves comprising *Avicenna marina* and *Aegiceras corniculatum* species (West *et al.*, 1985). Seagrass covers approximately 0.869 km^2 and includes *Zostera capricorni*, *Posidonia australis* and *Halophila* spp. with saltmarsh covering an area of 0.106 km^2 (West *et al.*, 1985).

Dredging activities have been undertaken in Port Hacking over much of the last century for shell grit mining, establishment of a fish hatchery at the entrance to Cabbage Tree Basin, and for maintenance of navigation channels (Meehan, 2001). Shell grit mining occurred from 1928 to 1973 and this combined with other dredging activities within the marine tidal delta, contributed to sedimentation and erosion of large areas of *Z. capricorni* and *P. australis* seagrass beds in Cabbage Tree Basin, Deeban Spit and Maianbar, between 1951 and 1975 (Meehan, 2001). Consequently, much of the intertidal sandflat areas included in the present research are now bare sandflats occupied by populations of *T. australiensis*.

Port Hacking is a popular leisure and tourist waterway, supporting a number of activities including boating and a large recreational fishery. Commercial fishing activities are not permitted within the waters of the estuary. Hand gathering of *T. australiensis* from intertidal sand/mud flats is permitted within the estuary and between the years 1991/92 to 2000/2001, the highest commercial catches of *T. australiensis* in NSW came from this location (NSW Fisheries, unpublished commercial catch data).

Plate 1.4. Port Hacking looking in an easterly direction towards the entrance. Courtesy of the NSW Department of Land and Water Conservation (Anon, 2004c).

Shoalhaven River

The Shoalhaven River is a mature barrier estuary located approximately 150 km south of Sydney (Fig. 1.2; Plate 1.5). It has a catchment area of 7,500 km^2 and a water area of 20 km^2 (West *et al.*, 1985). The main entrance to the Shoalhaven River is untrained and opens and closes intermittently, but has been closed now for many years. A second entrance is maintained through a man-made connection to the Crookhaven River approximately 5 km south, which has a trained permanent opening (Anon, 2004c). The river stretches some 300 km inland, with the lower 50 km affected by tides (Anon, 2004c). Mangroves (*A. marina* and *A. corniculatum*) cover an area of approximately 3.46 km^2. *Zosteraceae* spp. are the only seagrasses found in the system and cover an area of approximately 1 km^2. The area of saltmarsh within the system covers an area of approximately 1.54 km^2 (West *et al.*, 1985).

Land use surrounding the Shoalhaven flood plain was predominately classified as freehold agriculture (Bell and Edwards, 1980). In 2004, the Shoalhaven catchment remains one of the richest dairy regions in the state (Anon, 2004c). However, rapid population growth and development of new housing estates around major centres such as Nowra and Berry, has resulted in increased urbanisation of the catchment over the last 25 years. Much of this development has occurred on former agricultural land, with large areas of undisturbed Crown Land and State Forests still occurring on the escarpment and in the upper reaches of the river and catchment. Bell and Edwards (1980) estimated a moderate to high use and disturbance of the shoreline, with 25 - 50% of the catchment in natural condition.

It is likely that this estimate would lie below 25% today, given the increase in urbanisation.

Situated on the Shoalhaven/Crookhaven system are a number of popular holiday and tourist destinations including Shoalhaven Heads, Orient Point, Greenwell Point and Nowra. As a result, the river supports a large recreational fishery targeting finfish, molluscs, prawns and other crustaceans, including *T. australiensis*. The combined commercial fisheries production for the estuary is relatively large, with a total of 138,857 kg for the 2002/2003 financial year. Commercial catches of *T. australiensis* are small and have averaged only 77 kg per annum over the past decade, with no catches reported since 2000/2001 (NSW Fisheries, unpublished commercial catch data).

Plate 1.5. The permanently open entrance to the Crookhaven/Shoalhaven River system looking in a north-westerly direction. The intermittently open entrance to the Shoalhaven River is located immediately beyond the upper right hand corner. Courtesy of the NSW Department of Land and Water Conservation (Anon, 2004c).

Moruya River

The Moruya River is a mature barrier estuary located approximately 320 km from Sydney (Fig. 1.2, Plate 1.6.). It has a catchment of 1,549 km^2 and a water area of 30.4 km^2 (West *et al.*, 1985; Anon, 2004c). A permanently open entrance is maintained with twin training breakwaters. Water depths within the estuary are shallow, ranging from 2 - 3 m. The river stretches some 20 km inland before becoming the Deua River. *A. marina* and *A. corniculatum* mangroves cover a relatively small area (0.38 km^2). The seagrasses *Z. capricorni* and *Halophila ovalis* form an area of approximately 0.64 km^2. Areas of saltmarsh cover a combined area of 0.67 km^2 (West *et al.*, 1985).

The shoreline and water area of the Moruya River was classified as moderate to high use, with 25 to 50% of the shoreline in natural condition (Bell and Edwards, 1980). Again, this estimate is expected to be at the lower end of the scale today. Whilst a large proportion of the immediate shoreline area has been cleared for dairy farming and urban development, much of the catchment is contained within the Deua National Park, Crown Land, State Forests and relatively undisturbed freehold.

The Moruya River is in close proximity to the popular tourist destination of Batemans Bay, which lies approximately 20 km to the north. Many tourists undertake day trips to the river from Batemans Bay, although Moruya is a popular destination in its own right. Consequently, the estuary supports a significant recreational fishery and its rock-trained entrance provides an access point to inshore coastal waters. The river supports a small commercial fishery producing a

variety of finfish. The commercial fisheries production for 2002/2003 was 19,267 kg with no commercial catches of *T. australiensis* ever reported (NSW Fisheries, unpublished commercial catch data).

Plate 1.6. The entrance to the Moruya River looking in a westerly direction. Photograph courtesy of the NSW Department of Land and Water Conservation (Anon, 2004c).

1.7 Taxonomy of *Trypaea australiensis*

The Thalassinidea, commonly referred to as ghost or mud shrimp, are decapods found in coastal marine and brackish environments across most continents. Globally there are over 516 reported taxa, most of which (~95%) burrow in the substrata of shallow waters (0 – 200 m deep) (Dworschak, 2000). Smaller numbers of species live in reef cavities and inside corals and sponges, and only three species are found at depths greater than 2000 m (Poore and Griffin, 1979; Dworschak, 2000). Species diversity increases from high to low latitudes towards the equator, with similar numbers recorded from northern and southern hemispheres (Dworschak, 2000). Highest percentages of species have been recorded from the Indo-west Pacific (32%), the Atlantic southwest (22%), Indian Ocean (15.7%) and Pacific southeast (Dworschak, 2000). In other regions such as the northeast and northwest Atlantic and Pacific, and Mediterranean, species diversity is generally low (< 5% in most regions) (Dworschak, 2000).

In Australia, Poore and Griffin (1979) identified 40 species of thalassinid shrimp, 28 of which were endemic, and 24 of which occurred in more than three locations. Five main groupings were outlined including; a northern group extending south along the east coast; a southern group extending south along the west coast; a southern group extending east; and an eastern group distributed mainly along the south-eastern and eastern coasts. Several new species have been described since Poore and Griffin (1979), bringing the total to over 50 thalassinids for Australia (Sakai, 1984, 1988, 1993; Tudge *et al.*, 2000).

The systematic status and classification of the Thalassinidea has undergone much revision over the last century and is still a subject of some contention and debate (Borradaile, 1903; Poore and Griffin, 1979; Manning and Felder, 1991; Poore, 1994; Sakai, 1999; Tudge *et al.*, 2000; Tamaki, 2003), which is beyond the scope of this thesis. The phylogeny of Poore (1994) divides the Infraorder Thalassinidea into three superfamilies, 11 families and 73 genera (not shown):

Infraorder Anomura

Infraorder Thalassinidea

Superfamily Thalassinoidea Dana, 1852
Family Thalassinidae Dana, 1852

Superfamily Callianassoidea Dana, 1852
Family Laomediidae Borradaile, 1903
Family Upogebiidae Borradaile, 1903
Family Callianideidae Kossmann, 1880
Family Thomassiniidae Saint Laurent, 1979
Family Ctenochelidae Manning and Felder, 1991
Family Callianassidae Dana, 1852

Superfamily Axioidea Huxley, 1879
Family Calocarididae Ortmann, 1891
Family Axiidae Huxley, 1879
Family Strahlaxiidae fam. Nov
Family Micheleidae Sakai, 1992

In eastern Australia, *T. australiensis* is the most abundant thalassinid, occurring in estuarine sand and mud flats from northern Queensland to western Victoria. Although Dana (1852) originally described this species as *Trypaea australiensis*, other studies have often referred to *Callianassa australiensis* (Hailstone and Stephenson, 1961; Coleman and Poore, 1980; Nurse, 1980; Coleman, 1981; Kenway, 1981). According to Tudge *et al.*, (2000) this represents broad generic

application of the genus name, rather than misclassification. Hence, smaller genera within the Callianassidae including *Trypaea* represent specialised derivatives. A similar situation has occurred for another species in Australia, *Biffarius arenosa* (formerly *Callianassa arenosa*). In south-eastern NSW, *B. arenosa* does not appear to reach the same densities as *T. australiensis* (pers. obs), and is much smaller in size, with a total length of around 40 mm (Poore and Griffin, 1979). Small individuals of *T. australiensis* may be confused with adults of *B. arenosa* in field investigations relying on macroscopic identification. However, under a dissecting microscope, differences between the species are distinct and easily distinguished by the peduncle of antenna 1, which is shorter and stouter than the peduncle of antenna 2 for *B. arenosa* (Fig. 1.3a). For *T. australiensis,* the peduncle of antenna 1 is almost twice as long as the peduncle of antenna 2 (Fig. 1.3a). Another diagnostic characteristic that avoids confusion between the two species is the telson of *T. australiensis*, which is concaved medially on the posterior edge (Fig. 1.3b).

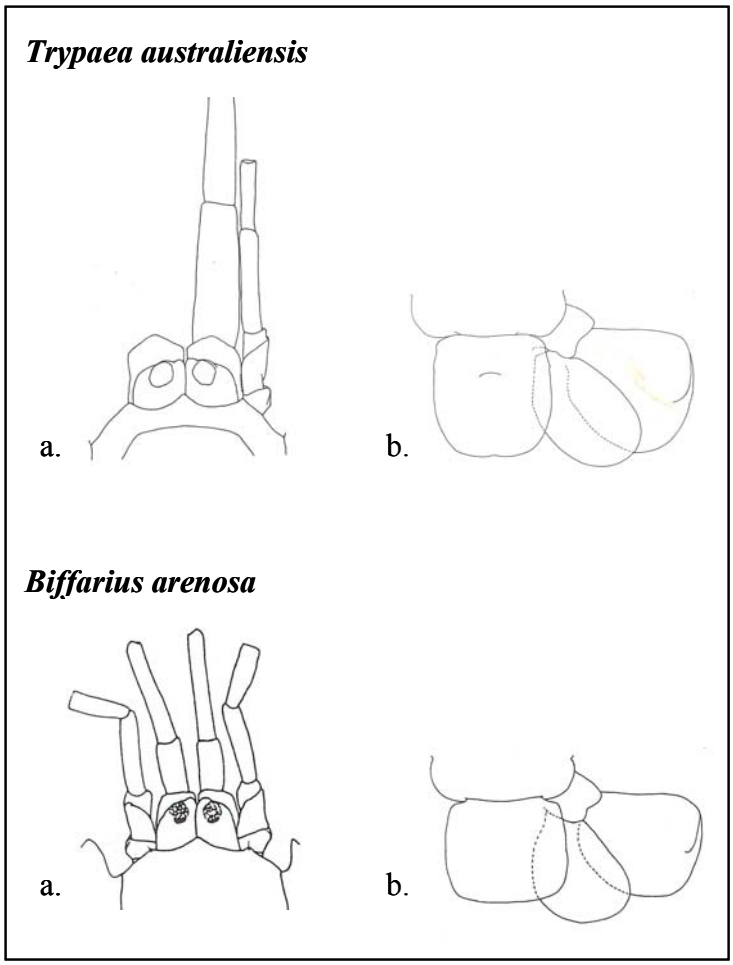


Figure 1.3. Line drawings of *Trypaea australiensis* and *Biffarius arenosa* (taken from Poore and Griffin, 1979) showing morphological differences between a) length of peduncle on antenna 1 and b) shape of telson. *B. arenosa* is referred to as *Callianassa arenosa* by Poore and Griffin (1979) and *B. arenosus* by Boon *et al.*, (1997); Bird *et al.*, (2000); Stapleton *et al.*, (2001).

Chapter 2

Comparison of methods for sampling populations of ghost shrimp, *Trypaea australiensis*

2.1 Introduction

Harvesting of intertidal ghost shrimp (Thalassinidea) by recreational anglers forms significant bait fisheries in many parts of the world (Hailstone and Stephenson, 1961; Forbes, 1977a; Wynberg and Branch, 1991). Often however, management of these harvested bait stocks is made difficult by lack of information, a situation exacerbated by difficulties in sampling burrowing shrimps. Previous studies have used manual suction pumps (Hailstone and Stephenson, 1961; Forbes, 1977a; Pezzuto, 1998), sediment cores (Devine, 1966; Tamaki and Ingole, 1993; Dumbauld *et al.*, 1996; Tamaki *et al.*, 1997; Berkenbusch and Rowden, 1998), shovels (Pohl, 1946; Dworschak, 1988), metal frames (Kevrekidis *et al.*, 1997), diver-operated suction samplers (Tunberg, 1986), weighted lines (Vaugelas *et al.*, 1986) and pump driven hydraulic jets (Felder and Lovett, 1989). Manual suction pumps and cores are most commonly used to sample ghost shrimp, but each may differ in sampling efficiency and bias. For example, Rowden and Jones (1994) argued that both pumps and cores selectively sample lighter females, as larger males are often found in the deeper galleries of burrows. The present study compared various methods of sampling the ghost shrimp *Trypaea australiensis*, a relatively abundant species found in the intertidal sand flats of many eastern Australian estuaries (Hailstone and Stephenson, 1961). Initially, optimum methods for coring (Experiment 1) and pumping (Experiment 2) were investigated. Then the coring method was

compared to the pumping method in terms of abundance estimates, size frequencies and sex ratios (Experiment 3). The studies were carried out in three large estuaries in south-eastern Australia, namely Port Hacking (34º05'S 151º09'E), Shoalhaven River (34º51'S 150º44'E) and Moruya River (35º55'S 150º09'E) (see Chapter 1).

2.2 Materials and methods

2.2.1 Experiment 1: Comparison of core size

Coring methods involved sinking 50 cm lengths of polyvinylchloride (PVC) tube into the sediment, excavating the contents with a hand trowel and sieving (1.56 mm mesh) to separate the ghost shrimp. In this experiment, two sizes of cores were compared: 0.04 m^2 (24 cm diameter) and 0.07 m^2 (29 cm diameter). Initial trials indicated that smaller cores were too narrow to excavate, that larger cores were too difficult to retrieve and that longer tubes would not penetrate the sediment. Two sites, 100 m in diameter and 100 m apart, were randomly selected from the extensive tidally exposed sandflats in Port Hacking (near Maianbar). Ten replicates of each core size were randomly sampled from each site at low-tide on two consecutive days in October 2000. Two-factor analysis of variance (ANOVA) was used to compare density estimates (catch per m^2) between core sizes and sites. Factors were considered fixed and data tested for normality and homogeneity of variances using Shapiro-Wilk and modified Levene's tests respectively. Student-Newman-Keuls (SNK) test was used to determine significantly different means. Efficiency was compared in terms of total "cost" of each method, calculated as the number of replicates required to give a precision

(SE/mean) of 0.2, multiplied by the average time taken to process each core (Andrew and Mapstone, 1987).

2.2.2 Experiment 2: Determination of suction pump effort

Ghost shrimp are a popular bait item in eastern Australia and a specialised pump used by recreational and commercial fishers, called a yabby pump, is sold widely. These pumps are a stainless steel tube, typically 75 cm in length and 50 mm in diameter, with an internal plunger attached to a handle. The pump is pushed into the sandflat (usually over burrow entrances) at an angle of approximately 10° and the plunger is pulled out, which creates suction. This sucking action forces a mixture of sand, mud, water and in some cases ghost shrimp, into the pump. The pump is then withdrawn from within the sandflat and the contents are expelled onto the surface, allowing any captured ghost shrimp to be removed. The process is usually repeated three or four times to the depth of the pump (i.e., 75 cm), or until no more ghost shrimp are found. This experiment was designed to select an appropriate unit of effort to quantitatively sample ghost shrimp with this suction pump. Twelve 0.1 m^2 quadrats were randomly selected on the sandflats in Port Hacking (see above). Within each quadrat, a single burrow was selected and pumped 4 times (to a final depth of 75 cm), then a second selected and pumped four times, then a third and fourth. In total, each quadrat was sampled with four, eight, 12 and 16 "pumps". ANOVA was used to compare mean numbers of individuals caught with the different pumping efforts (four, eight, 12 and 16 pumps). Data were checked for normality, homogeneity of variances (see previously) and means compared with SNK tests. Further data on the optimal number of pumps were collected from sites in the Moruya River. Here, the mean

numbers of animals caught using eight and 12 pumps were compared at 30 randomly selected quadrats at two sites (Garlandtown and Quondolo Island) using a *t*-test ($\alpha = 0.05$).

2.2.3 Experiment 3: Comparison of catches from coring and suction pumping methods

The abundance estimates, size frequencies and sex ratios of catches from cores and suction pumps were compared across all three estuaries (Port Hacking, Shoalhaven River and Moruya River) to determine the more effective method. Two sites, separated by at least 1 km were selected in each estuary. In December 2000 (8^{th} - 20^{th}), four replicate cores were taken from three randomly selected 10 m x 10 m plots at each site in each estuary, giving a total of 72 cores. In January 2001 (18^{th} – 31^{st}), three 10 m x 10 m plots were randomly selected from each site in each estuary and 7 replicate quadrats were pumped 12 times each (four pumps in each of three burrows), for a total of 126 quadrats. Logistic constraints prevented sampling with both methods during the same month. However, given that both coring and pumping were done only 29 days apart during summer, the impacts of time and season on the comparison were assumed minimal.

Further considerations in the comparison of catches from coring and pumping methods are related to the effects of tide and lunar periodicity. For example, at dead-low tide, the efficiency of both methods may decline due to difficulties in penetrating relatively dry surface sediments. For this reason, all sampling commenced on outgoing tides, a number of hours prior to low-tide (usually 2-3), when surface sediments were initially exposed and sufficiently wet. Hence, the

number of replicate cores and pumped quadrats was the maximum that could be completed within this period. Although comparisons between cores and pumps were made from samples collected across different moon phases, there are apparently no documented impacts of lunar periodicity on catches of burrowing thalassinid shrimp within the scientific literature. Whilst tidal amplitude is related to moon phase, differences in tidal range were considered unlikely to affect sampling efficiency, as populations were sampled with both methods at relatively the same point on outgoing tides (i.e., as sandflats became exposed), regardless of variation in minima and maxima. For example, on larger spring tides during the full moon, this simply required waiting until the tide was low enough to commence sampling.

Contents of cores and suction pumps were sieved (1.56 mm mesh) and ghost shrimp retained in snap-lock plastic bags and frozen. Catch per unit effort (CPUE) was calculated for each sampling event as numbers of individuals caught per minute, which allowed methods to be compared with a *t*-test (α = 0.05). A Kolmogorov-Smirnov two-sample test was used to determine if the length frequency distributions of samples caught by the two methods were significantly different. χ^2 - Tests were used to examine deviations in sex ratio from the expected value of 1:1 for the total number of animals, as well as for individual size classes. The mean length and weight of males and females were also compared using a *t*-test (α = 0.05).

2.3 Results

2.3.1 Experiment 1: Comparison of core size

There were no significant differences in the mean density of ghost shrimp between 0.04 m^2 and 0.07 m^2 cores (d.f. = 1, $F = 0.21$, $P > 0.05$), although the number of individuals caught varied significantly between sites (d.f. = 1, $F = 13.79$, $P < 0.05$, see Fig. 2.1). There were differences in the time taken to process each replicate, with the 0.04 m^2 core taking an average of 6 min less than the 0.07 m^2 core (Table 2.1). However, the precision of each core size varied between sites, the 0.07 m^2 core having greater precision compared to the 0.04 m^2 core at one site but vice versa at the second site (Table 2.1). Consequently, total cost of each core size was dependent on site (Table 2.1). Since the cost of the 0.04 m^2 core was more consistent between sites, this core size was chosen for future comparisons of catch between cores and the suction pump (Experiment 3).

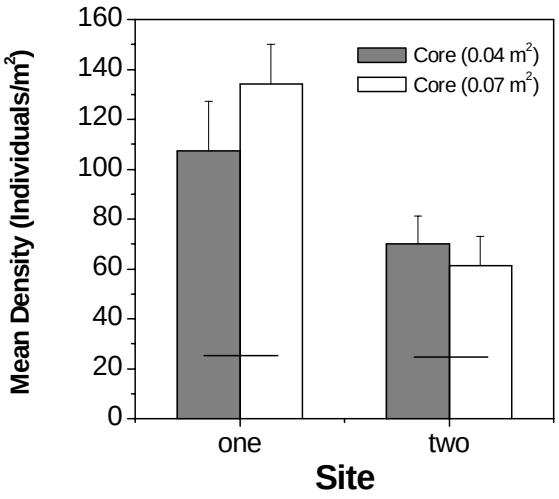


Figure 2.1. Mean density (individuals/m^2) of *T. australiensis* caught using a 0.04 m^2 and 0.07 m^2 cores at two sites at Maianbar, Port Hacking, in October 2000. Horizontal lines (SNK test) join means with no significant difference.

Table 2.1. Summary of data from a comparison of the numbers of ghost shrimp, *T. australiensis*, caught using different core sizes at two sites at Maianbar, Port Hacking, in October 2000. Abbreviations used: N.R = number of replicates required to give a precision of 0.2; rep. = replicate. Cost = N.R x mean time per replicate.

Core size	Replicates	Total ghost shrimp	Mean density (per m^2)	SE	Precision	N.R (p=0.2)	Mean time per rep.	Cost
Site 1								
0.04	10	43	107.5	19.7	0.18	8	12 min	96
0.07	10	94	134.2	15.9	0.12	4	18 min	72
Site 2								
0.04	10	28	70	11.1	0.16	6	12 min	72
0.07	10	43	61.4	11.7	0.19	9	18 min	162

2.3.2 Experiment 2: Determination of suction pump effort

At Maianbar in Port Hacking, 12 pumps yielded significantly more animals than four pumps (d.f = 3, F = 3.05, P < 0.05, Fig. 2.2). However, there were no significant differences between eight, 12 and 16 pumps respectively (Fig. 2.2). Hence each quadrat required a minimum of 8 pumps. Further sampling using eight and 12 pumps from the Garlandtown and Quondolo Island sites in the Moruya River revealed that significantly more individuals were caught from 12 pumps compared to eight pumps (t = 2.970, P < 0.01, Fig. 2.2). As a consequence, it was decided that 12 pumps of the suction pump in a 0.1 m^2 quadrat would be used in comparisons with the 0.04 m^2 core.

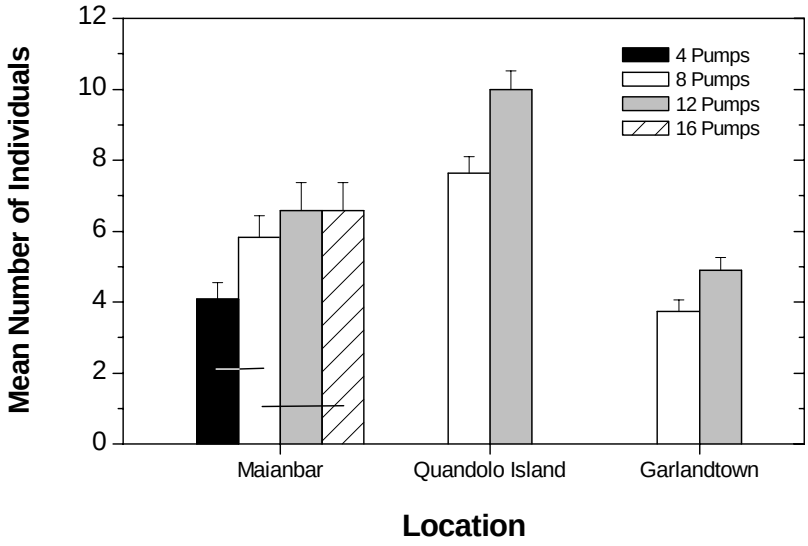


Figure 2.2. Mean (±SE) number of *T. australiensis* caught from 4, 8, 12 and 16 pumps respectively of a suction pump in 0.1 m^2 quadrats at Maianbar in Port Hacking, and from eight and 12 pumps respectively at Quondolo Island and Garlandtown in the Moruya River. Horizontal lines join means with no significant difference (SNK test).

2.3.3 Experiment 3: Comparison of catches from core and suction pump

The average time taken to complete a replicate sample using a core was 12 min, compared with 6 min using the suction pump. To allow comparisons of efficiency between methods, the number of individuals caught per replicate sample using each method was converted to number of individuals caught per minute. Data from all sites and estuaries were pooled and differences in the mean number of individuals caught between methods were compared (*t*-test). The suction pump was clearly the more efficient method, catching significantly greater numbers of ghost shrimp per minute than the core ($t = -8.589$, $P < 0.001$, Fig. 2.3).

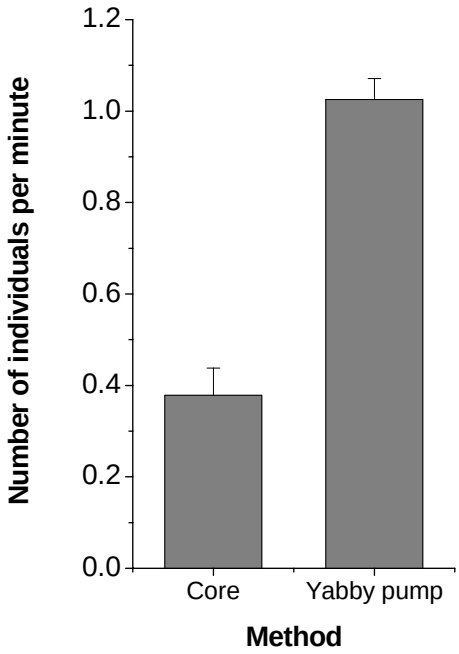


Figure 2.3. Mean (±SE) number of *T. australiensis* caught per minute from cores and a suction pump, combined across all sites in Port Hacking (Maianbar and Cabbage Tree Basin), Shoalhaven (Shoalhaven Heads and Old Man Island) and Moruya River (Garlandtown and Quondolo Island).

The size frequency distributions of *T. australiensis* differed significantly between the two sampling methods (Kolmogorov-Smirnov two-sample test; $Z = 0.113$, $P = 0.007$). Shapiro-Wilk tests indicated that the size frequency distributions of catches from the core and pump were both significantly different from normal ($P < 0.001$). However, catches from the pump displayed a more normal distribution, with individuals ranging between 2.8 and 14.9 mm carapace length (CL) (Fig. 2.4). Catches from the core revealed a bimodal distribution, with lengths ranging from 2.5 to 14 mm (CL) (Fig. 2.4). Larger individuals were poorly represented by the coring method, although a higher percentage of small individuals <5 mm (CL) were caught with this method.

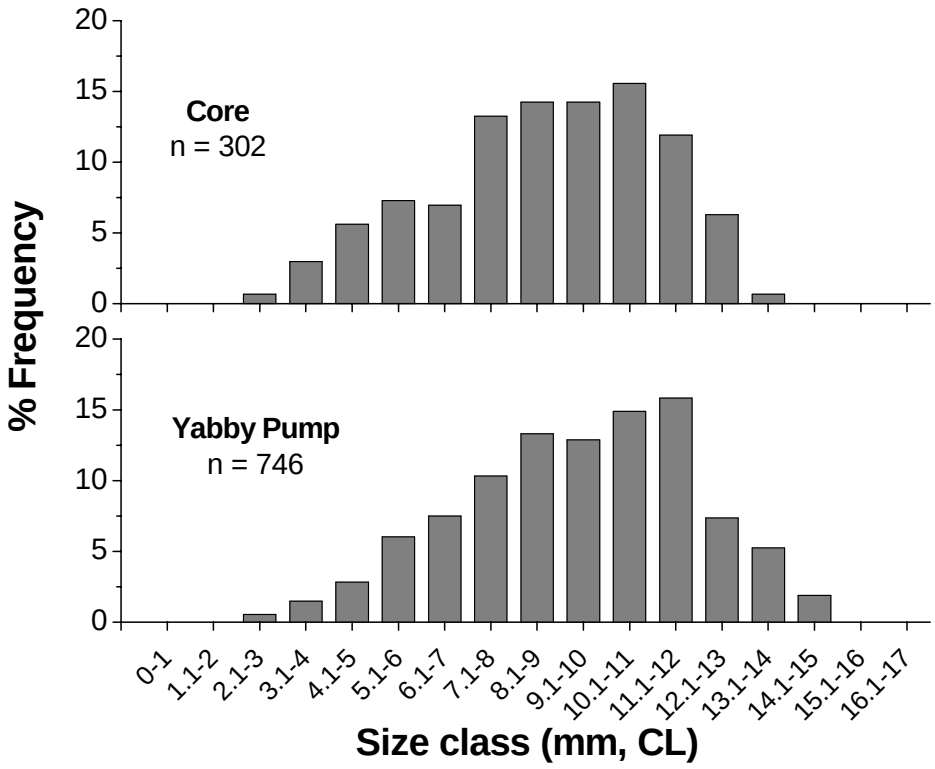


Figure 2.4. Size frequency distributions of *T. australiensis* caught from a core and a suction pump combined across sites in Port Hacking (Maianbar and Cabbage Tree Basin), Shoalhaven (Shoalhaven Heads and Old Man Island) and Moruya River (Garlandtown and Quondolo Island).

The male:female sex ratio of catches from the core, combined for all sites and locations, was 1:1. The only significant departure from the expected 1:1 ratio was in the 12.1-13 mm (CL) size class, which was male-biased (Table 2.2). In contrast, combined catches from the pump showed a sex ratio of 0.71:1 male:female, which was significantly different from the expected 1:1 ratio (χ^2 = 21.77; $P < 0.001$). Sex ratios were variable in the smaller and middle range of size classes, however larger size classes between 10 and 13 mm (CL) were all significantly female-biased (Table 2.2). The largest size class (14.1 - 15 mm, CL) was significantly biased towards males. The mean lengths and weights of males and females were compared from pump catches. Overall, the mean length of females was significantly larger than males (t = 2.823, $P < 0.05$), although there was no significant difference in the mean weight of males and females (t = 0.452, $P > 0.05$). The weights of males and females were also compared in the size classes that contained significantly female-biased sex ratios. Whilst the mean weight of males was significantly higher in the 10.1 - 11 mm (CL) (male = 1.75 g, female 1.71 g; t = -2.492, $P < 0.05$) and 12.1 - 13 mm (CL) size classes (male = 3.88 g, female = 3.15 g; t = -4.368, $P < 0.001$), there was no significant difference in wet weight between males and females in the 11.1 – 12 mm CL size class, which was the most female-biased (male = 2.56 g, female = 2.58 g; t = 0.173).

Table 2.2. Sex ratio of *T. australiensis* amongst different size classes. Asterisks indicate sex ratios significantly different from 1:1 (χ^2). Levels of significance: * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$).

Size class	Male:female ratio	
(mm, CL)	Core	Yabby Pump
3.1-4	2.5	1.33
4.1-5	0.75	0.91
5.1-6	0.61	1.81*
6.1-7	1.1	1
7.1-8	1.12	0.64
8.1-9	0.57	0.98
9.1-10	1.52	0.81
10.1-11	0.74	0.5***
11.1-12	0.84	0.25***
12.1-13	3.75*	0.45**
13.1-14	2	1.6
14.1-15	-	3.6*

2.4 Discussion

Previous studies of ghost shrimp have used a variety of core sizes (Devine, 1966; Tamaki and Ingole, 1993; Dumbauld *et al.*, 1996; Tamaki *et al.*, 1997; Berkenbusch and Rowden, 1998), however none have involved comparisons of core size. In this study, there were no consistent differences in numbers of *T. australiensis* caught by the two different sized cores (Fig. 2.1), nor in precision. However, total estimated cost of sampling with the smaller core (0.04 m^2) was similar at each site sampled and it was chosen for further comparisons between catches from the pump. Sampling ghost shrimp with suction pumps is often done (see Hailstone and Stephenson, 1961; Forbes, 1977a; Pezzuto, 1998), but is not quantitative unless a standardised measure of catch per unit effort can be obtained. Forbes (1977a) recorded the number of prawns per 100 pump strokes from the Swartkops Estuary in South Africa as a quantitative estimate of monthly abundance. The present study expanded on this methodology by selecting random sampling locations and optimising the number of pumps within a 0.1 m^2 quadrat. In this case, 12 pumps (four pumps from each of three burrows) were found to be optimal (Fig. 2.2). Although sampling efficiency of the operator conducting the 12 pumps may have improved during initial stages of the experiment (perhaps through increased pumping speed), the fact that more than 1700 pumps had been done on completion of the study, suggests that further improvement in operator efficiency over longer temporal scales is unlikely, or minimal at best.

The comparative experiment clearly demonstrated that suction pumping was more efficient than coring for sampling *T. australiensis*, with more than twice the number caught pumping during the same period of time (Fig. 2.3). In addition,

fewer individuals were damaged when pumping, compared to the coring and excavating method (pers. obs). Another problem related to the coring method, was that excavation created a vacuum causing cores to drag in surrounding sediment and ghost shrimp. As a result, density estimates from cores may be misleading. Size frequencies also varied significantly between methods. Pump catches displayed a more normal distribution and contained size classes from post-larval recruits through to large adults (Fig. 2.4). Smaller size classes were also represented in catches made by the corer, but larger individuals were notably absent. While this could be a product of relatively shallow penetration of cores (Rowden and Jones, 1994), it may also be a result of the excavation time (12 mins), which could allow large males to evade capture.

Overall, the male:female sex ratio of catches from the core was 1:1, whilst samples from the yabby pump were biased towards females (0.71:1). Female-biased sex ratios are characteristic of thalassinid shrimps and are consistent across different habitats, depths and methods (see Pezzuto, 1998). Rowden and Jones (1994) suggested that pumps might selectively sample lighter females. In the present study, there were no differences in mean weight between sexes. However, in catches from the pump, two of the female-biased size classes (Table 2.2), contained males that were significantly heavier than females. In comparison, the most heavily female-biased size class contained no differences in weight between males and females. Considering that pumps can extract around 2.45 kg of sediment (dry mass) in one pump (Wynberg and Branch, 1991), it would seem unlikely that differences of less than 1 g between males and females in some size classes would result in higher catches of females. Moreover, the largest size

classes were in fact, male-biased, which demonstrates that unlike the core, the suction pump was capable of sampling even the heaviest and deepest burrowing males.

The present study has shown that suction pumps (in conjunction with fine-meshed sieves) are an effective method of sampling populations of *T. australiensis*. Indeed, it proved a more efficient method compared to sampling with cores, with field collections conducted in less than half the time. This allowed greater replication to be incorporated into the experimental design and resulted in larger sample sizes. Furthermore, catches from these pumps represented a wider range of ghost shrimp, from newly recruited individuals through to large adults, and contained fewer damaged individuals compared to catches from the core. Although pump catches were biased towards females, it is unlikely that this resulted from the selectivity of the method and instead, reflected sex ratios which are characteristic of thalassinid populations.

Chapter 3

Spatial and temporal patterns of distribution and abundance of *Trypaea australiensis* in south-eastern Australia

3.1 Introduction

Quantifying variability in the distribution and abundance of organisms, at a range of appropriate spatial and temporal scales, is fundamental to the formulation of hypotheses that explain patterns in ecology and to the assessment and management of anthropogenic impacts (Andrew and Mapstone, 1987; Levin, 1992; Underwood, 1992). In marine systems, abundances of species are often patchy at a range of different spatial scales, as a result of variability in physical environmental conditions (e.g., waves, currents, tidal exposure) (Bustamante and Branch, 1996; Bell *et al.*, 1997; Chapman, 2000), biological processes (e.g., behaviour, recruitment, competition and predation) (Dayton, 1971; Menge, 1978a, b; Hawkins and Hartnoll, 1982; Connell and Keough, 1985; Jernakoff, 1985a, b; Fairweather, 1988, 1990a; Chapman and Underwood, 1994; Chapman, 1995; Chapman and Underwood, 1998; Chapman, 2000), natural and anthropogenic disturbances (Fairweather, 1990b; Underwood, 1999; Bishop *et al.*, 2002) and habitat complexity and availability (Chapman, 1994a; Archambault and Bourget, 1996; Thompson *et al.*, 1996). Consequently, abundances of marine organisms may display large-scale variability between shores (or sandflats, headlands, estuaries etc), to small-scale variability between sites within shores and between replicate quadrats within sites (Morrisey *et al.*, 1992a; Underwood and Chapman, 1998a). Abundances also vary over short-term (days, weeks, months) and long-term (seasons, years) scales and different temporal patterns may exist at different

spatial scales (Morrisey *et al.*, 1992b; Thrush *et al.*, 1994; Aberg and Pavia, 1997; Underwood and Chapman, 1998b, c). Hence, comparisons of abundance at broad spatial and temporal scales (e.g., sandflats, shores, estuaries, headlands and seasons, years etc) are not valid unless within-scale variability has been measured (Hurlbert, 1984; Stewart-Oaten *et al.*, 1986).

Hierarchical or "nested" sampling designs are one method of measuring and comparing variability in abundance of species at multiple scales. These designs overcome the problem of confounding or "pseudoreplication" (after Hurlbert, 1984) by consecutively nesting each successive scale within a larger scale. Previous studies have measured and compared variations in abundance at several spatial and/or temporal scales using hierarchical designs for a variety of marine organisms and assemblages (Caffey, 1985; Jones *et al.*, 1990; Fairweather, 1991; Kennelly and Underwood, 1992; Morrisey *et al.*, 1992a; Morrisey *et al.*, 1992b; Ferrell *et al.*, 1993; Chapman, 1994b; Underwood and Chapman, 1996; Gillanders, 1997; Underwood and Chapman, 1998b; Kendall and Widdicombe, 1999; Menconi *et al.*, 1999; Chapman, 2002; Olabarria and Chapman, 2002). Still, there has been a general reluctance to conduct or publish observational studies testing hypotheses about patterns, as ecological studies have traditionally focussed on investigating processes using manipulative experiments (Underwood *et al.*, 2000). Underwood *et al.* (2000) maintains that testing hypotheses about processes without knowledge of patterns is illogical, and well structured observational or "mensurative" studies (after Hurlbert, 1984) warrant the same recognition in the ecological literature as manipulative experiments. Indeed some scientific fields, such as the assessment and management of fisheries resources, depend upon

observational studies investigating patterns of distribution and abundance (Underwood *et al.*, 2000).

Despite a world-wide distribution (Felder, 2001) and being an obvious component of many soft-sediment habitats, patterns of abundance of burrowing thalassinid shrimp are poorly understood. Previous studies of thalassinids have generally focused on other aspects of biology and ecology, with few quantitative accounts of abundance (Table 3.1). This is most likely due to the difficulty in obtaining large, representative samples as discussed in Chapter 2. Burrow counts are often used as surrogate estimates of abundance (Hailstone and Stephenson, 1961; Branch and Day, 1984; Vaugelas *et al.*, 1986; Cockroft and Tomalin, 1987; Hanekom *et al.*, 1988; Wynberg and Branch, 1991; Dumbauld *et al.*, 1996; Souza *et al.*, 1998). However, some studies have shown the relationship between burrow openings and abundance to be highly variable for thalassinids (McPhee and Skilleter, 2002a) and indeed other crustaceans (McKillup and Butler, 1979; Warren, 1990).

Although a number of researchers have quantitatively sampled populations of thalassinid shrimp, studies have generally been restricted to single sites, estuaries and/or locations (Table 3.1). As far as could be determined, there are no available published accounts of the distribution and abundance of any thalassinid species simultaneously over multiple spatial and temporal scales. Moreover, previous studies of abundance at single sites or locations have often not sampled appropriately; having either too few replicates spread over a large area, or having

Table 3.1. Summary of previous studies that have quantitatively sampled thalassinid shrimp abundance.

Species	Location	Spatial Scale/s	Temporal Scale/s	Sampling Frequency	Sampling Method	Reference
Trypaea australiensis & Callianassa arenosa	Western Port, Australia	Stations within single estuary	none	Single occasion	Digging out quadrats	Coleman and Poore, 1980
Trypaea australiensis & Callianassa arenosa	Western Port, Australia	Single site within single estuary	12 months	Monthly	Sampling frame	Coleman, 1981
Trypaea australiensis	Moreton Bay, Australia	Sites within a single shore	2 years	Six times	Yabby pump	McPhee and Skilleter, 2002a
Callianassa filholi	Otago Harbour, New Zealand	Single site	18 months	Monthly	Core	Berkenbusch and Rowden, 1998
Callianassa japonica	Kyushu, Japan	Stations along a single transect	10 years	8 times intermittently	Core, metal frame	Tamaki and Ingole, 1993
Callianassa japonica	Kyushu, Japan	Stations along a single transect	2 years	27 times – monthly-bi-monthly	Core	Tamaki *et al.*, 1997
Callianassa kraussi & Callianassa gilchristi	Algoa Bay, South Africa	Transects within a single bay	none	Single occasion	Diver operated suction sampler	Cockroft and Tomalin, 1987
Upogebia Africana & Callianassa kraussi	Swartkops Estuary, South Africa	Transects within single estuary	none	Single occasion	Digging quadrats & diver operated suction sampler	Hanekom *et al.*, 1988
Upogebia africana	Knysna Estuary South Africa	Sites within a single estuary	none	Single occasion	Digging out quadrats	Hodgson *et al.*, 2000a
Upogebia pusilla	Evros Delta, Greece	Single site	12 months	Monthly	Metal frame	Kevrekidis *et al.*, 1997
Upogebia deltaura	Bredholmen, Sweden	Single site	17 months	Fortnightly-monthly	Diver-operated suction sampler	Tunberg, 1986
Callianassa subterranea	Southern North Sea	Single site	27 months	Six occasions	Box corer	Witbaard and Duineveld, 1989
Callianassa subterranea	Southern North Sea	Stations within single site	3 years	Twice per year	Box corer	Rowden and Jones, 1994
Neotrypaea californiensis & Upogebia pugettensis	Willapa Bay, USA	Sites within single bay	4 years	Bimonthly and/or annual	Core	Dumbauld *et al.*, 1996

sufficient replicates but only within a single relatively small area, or insufficient replicates within small areas. For example, Berkenbusch and Rowden (1998) sampled *Callianassa filholi* in Otago Harbour, New Zealand using 6 - 9 cores (0.25 m^2 in size) over a relatively large 0.25 km^2 area; Tamaki and Ingole (1993) sampled *C. japonica* at 3 stations along one single transect for an entire sandflat in western Kyushu, Japan; and Rowden and Jones (1994) sampled *C. subterranea* in the southern North Sea using only a single replicate box-core for each of 5 sampling stations.

Poor sampling design and/or restricted spatial and temporal scales are also common for previous studies of *T. australiensis* in Australia. For example, Coleman and Poore (1980) quantitatively sampled the distribution and abundance of *T. australiensis* in Western Port (Victoria), in nine different sediment strata. Whilst there was considerable spatial replication in this study, sites were sampled on only one occasion. Coleman (1981) provided monthly abundance data on *T. australiensis* for a 12-month period at the same location, however sampling was restricted to a single site. Recently, McPhee and Skilleter (2002a) sampled populations of *T. australiensis* in three 1 ha (100 m x 100 m) sites on the western shore of North Stradbroke Island (Queensland, Australia). Within each site, ten to fifteen 2 m x 2 m replicates were sampled using a yabby pump, similar to the method described previously (see Chapter 2). Their experimental design however, does not give any meaningful insight into patterns of abundance over a range of scales, or to the potential processes controlling abundance, due to the large sizes of the sites and replicates that were used (see above). Hence, results can only be interpreted for a spatial scale of tens to hundreds of metres (i.e., between sites) as

any variability in the abundance of *T. australiensis* at smaller scales within sites (i.e., from 1 m to 100 m) was confounded within the residual (between replicate) variance. Furthermore, sampling was too infrequent to adequately document temporal patterns of abundance, as there were only six sampling occasions over an entire two-year period.

Clearly, there is a wide gap in knowledge regarding spatial and temporal patterns of abundance for *T. australiensis* and burrowing shrimp in general. This is surprising considering the importance of thalassinids to ecological processes such as bioturbation (Posey, 1986; Berkenbusch and Rowden, 1999; Berkenbusch and Rowden, 2003) and to commercial and recreational bait fisheries (Hailstone and Stephenson, 1961; Wynberg and Branch, 1991). Previous studies of other soft-sediment fauna have identified variability in abundance at a hierarchy of spatial and temporal scales (Morrisey *et al.*, 1992a; Morrisey *et al.*, 1992b), with the patchy distribution of fauna within sandflat habitats receiving much attention (Thrush, 1991; Thrush *et al.*, 1994; Thrush *et al.*, 1997). Similar patchiness in abundance may be expected for *T. australiensis*. However, any such variability in space or through time needs to be understood in order to determine the impacts of harvesting, and to assist in the decision making process for traditional fisheries management, and for ecosystem approaches to conservation of stocks, such as Marine Protected Areas (MPA's).

This chapter describes two studies related to spatial and temporal variation in abundance of *T. australiensis*. The first study relates to patterns of abundance over a hierarchy of spatial scales (from m to hundreds of km) and examines differences

in spatial pattern over time. The second study examined temporal patterns of abundance at a hierarchy of temporal scales (months to years) at one particular site in order to unconfound comparisons over time. In both studies, the general hypothesis tested was that the abundance of *T. australiensis* differed significantly at each of the spatial and temporal scales investigated. A second aim of this chapter was to investigate the relationship between burrow openings and abundance of *T. australiensis* over multiple spatial and temporal scales.

3.2 Materials and methods

3.2.1 Study location and sites

The study was conducted between Port Hacking and Moruya on the south-eastern coast of NSW (see Fig. 1.1 in Chapter 1). The estuaries sampled included Port Hacking, and the Shoalhaven and Moruya Rivers', which are described in Chapter 1. Within each estuary two sandflat sites separated by at least 1 km were selected and included; Maianbar and Cabbage Tree Basin in Port Hacking (Fig. 3.1 and Appendix 3), Shoalhaven Heads and Old Man Island in the Shoalhaven River (Fig. 3.2 and Appendix 3) and Garlandtown and Quondolo Island in the Moruya River (Fig. 3.3 and Appendix 3).

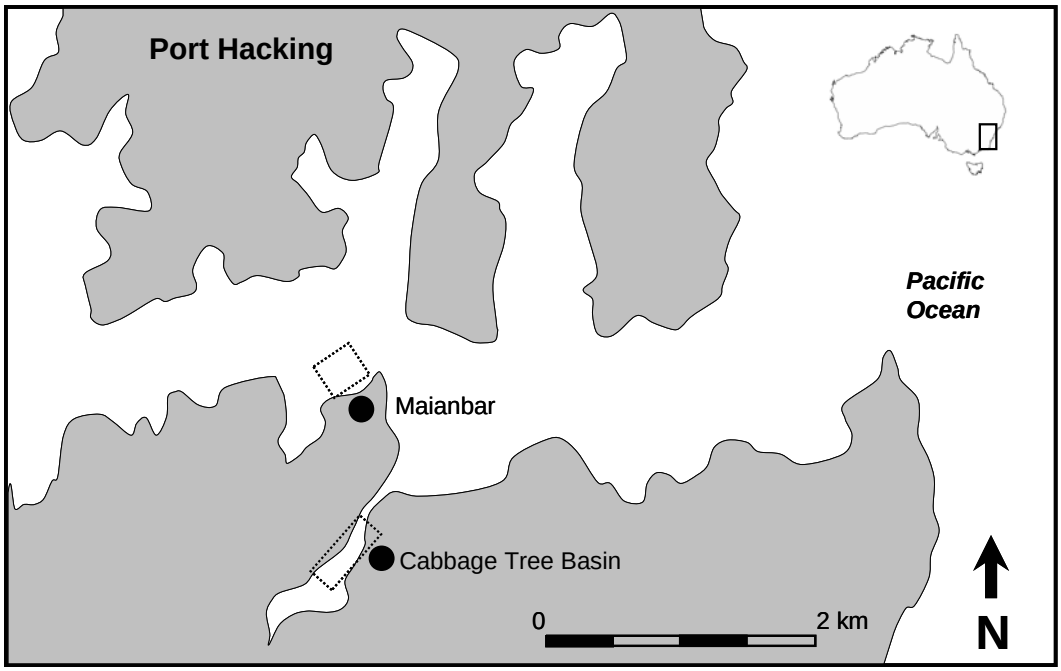


Figure 3.1. Locations of sampling sites at Maianbar and Cabbage Tree Basin in Port Hacking. Dotted lines indicate approximate area of sampling sites.

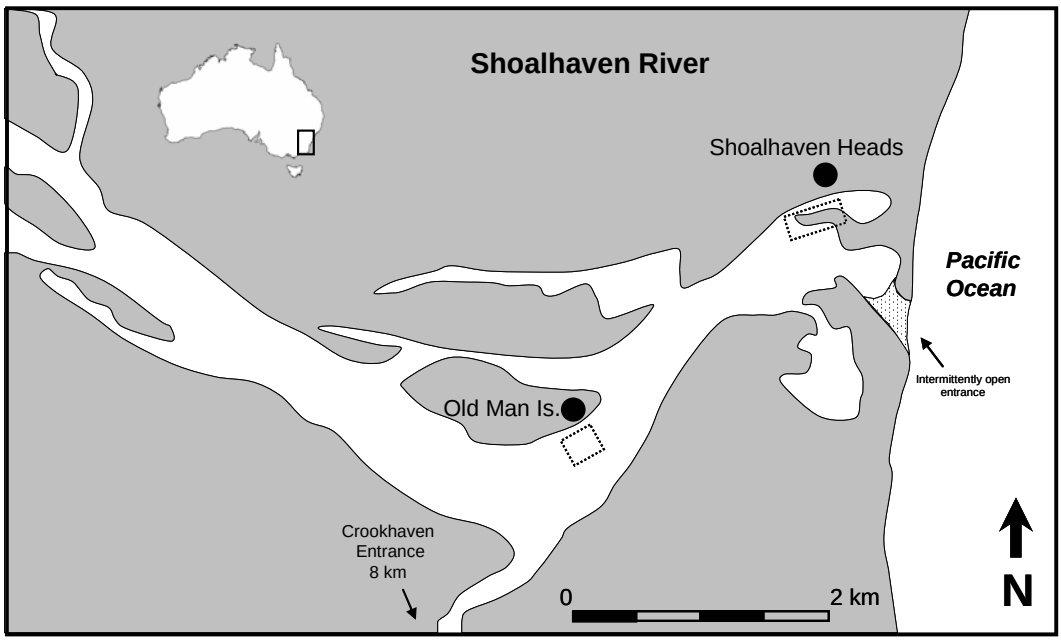


Figure 3.2. Locations of sampling sites at Shoalhaven Heads and Old Man Island in the Shoalhaven River. Dotted lines indicate approximate area of sampling sites.

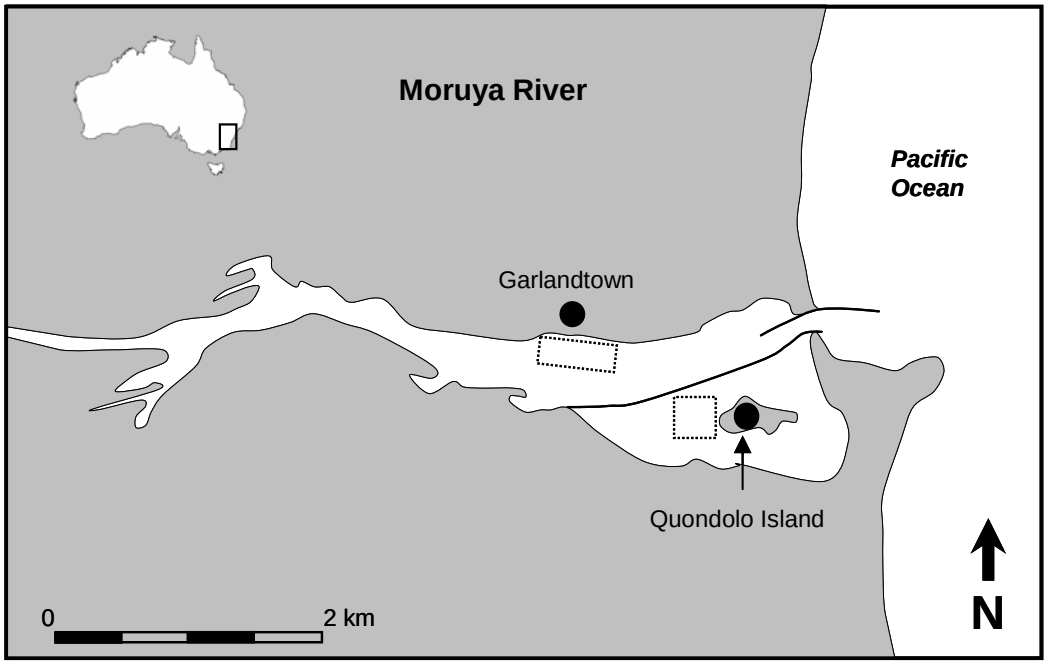


Figure 3.3. Locations of sampling sites at Garlandtown and Quondolo Island in the Moruya River. Dotted lines indicate approximate area of sampling sites.

3.2.2 Experimental design

To investigate spatial and temporal patterns of abundance of *T. australiensis*, a hierarchical sampling program was established using the sampling method previously described (see Chapter 2). Within each site in each estuary, three 10 m x 10 m plots separated by 50 m to 100 m were randomly selected. In each plot, five random 0.1 m^2 quadrats were placed, separated by at least 1 m. Twelve pumps of a yabby pump were done in each quadrat. Although 7 quadrats were sampled from each plot during the pilot study (Chapter 2), analysis indicated a similar power could be obtained from 5 quadrats (Fig. 3.4). Also, five quadrats ensured all sampling was conducted on the outgoing tide, as the potential exists for differences in abundance at different stages of the tidal cycle due to behavioural characteristics of the animal in relation to tidal movement (Kenway, 1981).

The experimental design incorporated nested spatial scales which ranged from metres (between quadrats), tens to hundreds of metres (between plots), kilometres (between sites within estuaries) and hundreds of kilometres (between estuaries) and thus avoided problems of pseudoreplication (see Hurlbert, 1984) (Fig. 3.5). Sampling was stratified at each site to include the intertidal zone where *T. australiensis* occurred. Unlike rocky shores, which are multi-scalar and can undergo significant changes in elevation within a few metres, vertical zonation in tidal flats is often less obvious given their planar nature and larger size. Hence, variation between plots in the present study represents within-site variation and no attempt was made to examine vertical differences in abundance.

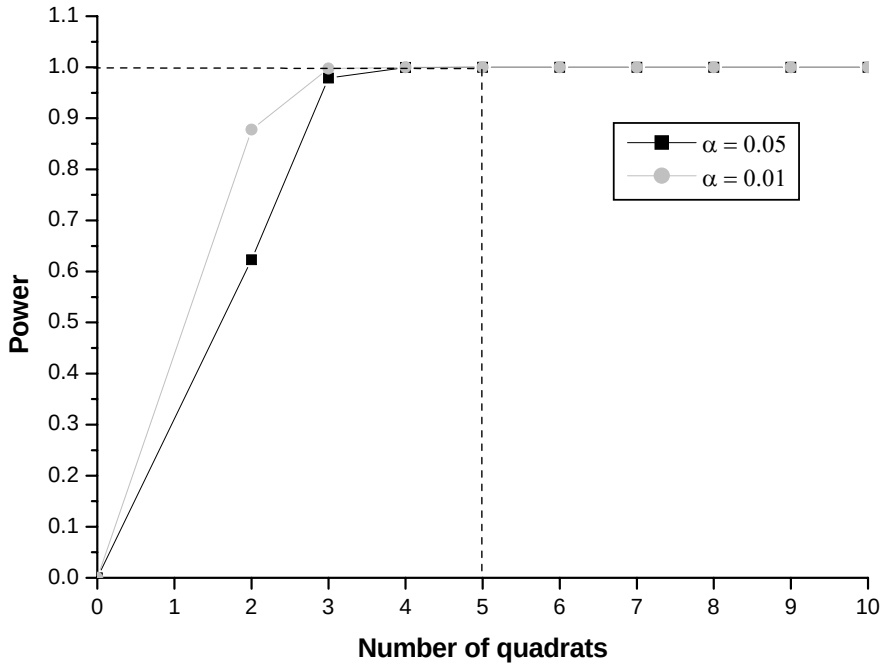


Figure 3.4. Results of power analysis showing number of replicate quadrats required to achieve a power of 1 at α = 0.05 (black line) and α = 0.01 (grey line) respectively.

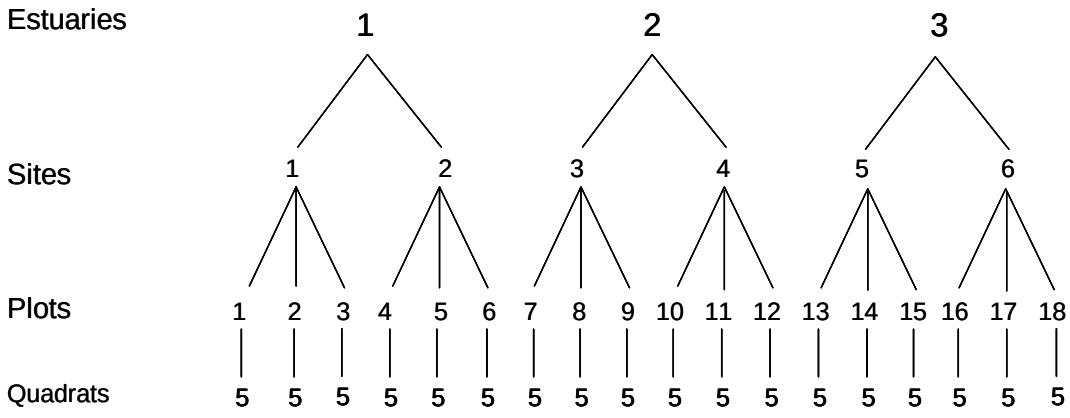


Figure 3.5. Diagrammatic representation of spatial scales sampled in the present study.

At the plot scale, the size of the areas chosen (10 m x 10 m) ensured recreational harvesters did not encroach during the sampling process. McPhee and Skilleter (2002a) used 1 ha areas (100 m x 100 m) at North Stradbroke Island in Moreton Bay (Queensland), where intertidal flats stretch some 10 km. However, areas of this magnitude are not typical of popular harvesting areas in south-eastern Australia. For example, Maianbar in Port Hacking is approximately 0.25 km^2 (500 m x 500 m) in size. Also, the sites sampled by McPhee and Skilleter (2002a) are generally less accessible to the public, ensuring minimal interference by anglers during the sampling process, unlike most sites in the present study. Such large sampling areas would certainly not be appropriate in south-eastern Australia, as they would not allow sufficient replication, given the comparatively small size of sites. Also keeping recreational fishers out of such large areas during the sampling process would prove difficult. In the present study, 10 m x 10 m plots were easy to manage, allowed sufficient replication across sandflats and generally reflect scales at which harvesting is carried out by amateur fishers.

Sampling was conducted at all spatial scales over a two-year period, monthly for the first 12 months and quarterly for the second 12 months, except for April 2002 which was not sampled. To investigate differences in abundance between years with respect to the amount of variation between months within years, the Maianbar site was sampled on a monthly basis for the entire two-year period. Sampling of all spatial scales at each time was generally conducted over a 3 to 5 day period on outgoing tides, with sampling generally commencing two hours before low-tide when sandflats became exposed. The delay in tides between sites within individual estuaries often allowed sampling of both sites on the same day.

However, weather extremes and availability of resources sometimes prevented sampling of two sites on the same day.

While the same 10 m x 10 m plots were sampled at each site on each occasion, random placement of the quadrats ensured independence of samples between times and the same quadrats were not sampled on each occasion. It has been suggested that repeated random sampling of the same areas in soft-sediment habitats may lead to experimental artefacts, as surrounding animals could be shifted due to infilling of holes caused by the sampling method, and result in increased vulnerability to predators (Skilleter, 1996). However, in the present study, the plots were located in sites that were also harvested by recreational fishers for bait and although the methodology did not result in large holes, it is assumed that artefacts of pumping (both experimental and recreational) would be similar across an entire sandflat. In addition, considering that pumping was done during low-tide periods and assuming that surrounding animals remain buried, an increase in predation from humans, fish and birds was considered unlikely.

3.2.3 Sampling of T. australiensis

On each sampling occasion, 12 pumps of the yabby pump were done in each 0.1 m^2 quadrat. Prior to pumping the quadrat, the numbers of burrow openings were counted to investigate the relationship between number of burrows and CPUE. Contents of the pump were sieved over 1.56 mm mesh and shrimp retained in snap-lock plastic bags and frozen. In the laboratory, animals were defrosted and measurements were taken which included; sex (presence absence of pleopods), total length (TL), carapace length (CL), chela height (ChH), chela width (ChW),

handedness (enlarged chela left or right), wet weight (to 0.01 g), macroscopic appearance of ovaries through transparent exoskeleton, presence of eggs attached to pleopods and egg stage (i.e., eyed or uneyed). All morphometric measurements (i.e., CL, TL, ChW, and ChH) were done using digital vernier callipers to 0.01 mm. This sampling program and observations also form the basis of chapters on reproduction (Chapter 4) and growth (Chapter 5).

3.2.4 Environmental data

Environmental variables were measured concurrently with sampling of ghost shrimp on most occasions. Salinity (parts per thousand, ppt) and water temperature (°C) were measured in mid-depth water adjacent to the sampling site with a handheld MC-84 meter. At times when the MC-84 meter was not available, water temperature was measured using a mercury thermometer and a sample of water was collected to allow salinity to be measured in the laboratory. Missing data for some sampling occasions was the result of the meter malfunctioning and the absence of an alternative method such as a mercury thermometer and water collection vessel. Environmental data were not collected for the extra months sampled at Maianbar.

3.2.5 Statistical analyses

Spatial patterns of abundance over a temporal period of two years were examined using analysis of variance (ANOVA). The total number of individuals, burrows, biomass, males and females, recruits (≤5 mm, CL) and the number of bait-sized individuals ≥7 mm (CL) were determined for each quadrat at each sampling time.

Data were analysed using a nested and orthogonal analysis of variance model. Spatial scales were random, nested factors that were orthogonal to time (a random factor). Time was considered a random factor as the general hypothesis tested was that abundance of *T. australiensis* changed through time. The model did not allow construction of a conventional *F*-ratio for the estuary and site factors. However, *post-hoc* pooling of higher order interactions involving the factors that were not significant with $P > 0.25$, allowed a standard *F*-ratio to be used (Winer *et al.*, 1991). When *post-hoc* pooling of interactions could not be done, the analysis proceeded as if interaction terms were significant, in which case no test was done (Underwood, 1997).

Data were tested for normality and homogeneity of variances using Shapiro-Wilk and modified Levene's tests respectively. Levene's test is considered better than Cochran's test in situations where data are not normally distributed, which was generally the case. Data were not transformed for violations of the assumption of normality, as ANOVA is considered robust to such violations in large balanced designs (Underwood, 1997). Heterogeneous data were transformed to *log* (x+1) where necessary, however, in situations where data remained heterogeneous even after transformation, the significance level was set to $P = 0.01$ to reduce the probability of incurring a Type 1 error (Underwood, 1981). Multiple comparisons of means were performed using Student-Newman-Keuls (SNK) tests.

Temporal persistence of spatial patterns of abundance was investigated for the total number of individuals, number of individuals ≥7 mm (CL) and number of recruits (≤5 mm, CL) using separate nested ANOVA's for each sampling

occasion, for the first 12 months. Hierarchical ANOVA allows a quantitative measure of variation associated with each factor in the analysis. Variance components were calculated using observed mean squares to estimate terms identified in the expected mean squares. Negative variance components were dealt with using the method of Fletcher and Underwood (2002), which gives equivalent results to residual maximum likelihood (REML) procedures. The percentage of variation for each level in the analysis was calculated as the component of variation divided by the sum of all components of variation and multiplied by 100. Investigations of temporal patterns at a hierarchy of scales was not possible across all spatial scales, as populations were sampled monthly for the first twelve months and quarterly for the second year. However, the Maianbar site was sampled approximately monthly for the entire two-year period, with an equal number of monthly samples in each year. Hence, temporal patterns of abundance (total number of individuals, burrows, biomass, males, females, recruits ≤5 mm and individuals ≥7 mm, CL) at scales less than two years (i.e., between months and years) and between plots at Maianbar were investigated using ANOVA. Month was nested within year and both factors were orthogonal to plots. All factors were considered random. *F*-ratios for the main effect of year were constructed by *post-hoc* pooling of non-significant interaction terms where $P > 0.25$ (see above). Assumptions regarding normality and homogeneity of variances were tested using the methods described above. Differences between means were investigated using SNK tests.

The relationship between number of burrow openings (dependent variable) and relative abundance of *T. australiensis* was investigated using linear regressions.

Analysis of covariance (ANOVA) examined whether the relationship between the number of burrows and relative abundance changed through time and between sites. Multiple regression analyses were used to examine the influence of environmental variables (salinity and temperature) on the mean abundance of ghost shrimp.

In this thesis, the terms “relative abundance” and “mean abundance” are used interchangeably to describe mean catch per unit effort (CPUE).

3.3 Results

3.3.1 Environmental data

The ranges of water temperatures were similar across sites, although seasonal minima and maxima were predictably lower at locations further south (Fig. 3.6 Table 3.2). The lowest temperature recorded was 12°C at Shoalhaven Heads in August 2003, whilst the highest recorded temperature was 30.2°C at Maianbar in January 2001. Similarly, mean temperatures were higher at the northern most sites compared to estuaries further south. Temperatures were in fact higher at sites in the Moruya River compared to the Shoalhaven, which lies further south of latter estuary. However, sites in the Shoalhaven were situated further upstream than locations in other estuaries, as the entrance was closed throughout the study period and tidal exchange was dependent on the Crookhaven entrance, some 8 km away (see Plate 1.4 and Fig. 3.2). The fact that temperatures within estuaries can range significantly above and below adjacent ocean waters has been well documented. Hence, the lower temperatures at sites within the Shoalhaven compared to the

Moruya River during winter months might be explained by a more restricted oceanic influence.

Salinity measurements were typical of marine dominated estuaries with mean salinity across all sites greater than 27 ppt (Table 3.2). However, temporal minima and maxima appeared to be seasonal, with the lowest salinity measurements recorded during late winter to early spring and highest values during the summer months (Fig. 3.6). The lowest salinity measurements were recorded at sites in the Shoalhaven River (Table 3.2), however as mentioned above, this is probably related to a lower marine input in this estuary compared to other locations.

Table 3.2. Summary of environmental data. Minimum, maximum and mean (±SE) salinity and temperature measurements at each site between January 2001 and January 2003.

Site	**Salinity**			**Temperature**		
	Min	Max	Mean (±SE)	Min	Max	Mean (±SE)
Maianbar	25.2	36.7	33.76 (0.94)	12.5	30.2	21.08 (1.47)
Cabbage Tree Basin	28.4	37	34.18 (0.57)	12.4	27.8	20.80 (1.20)
Shoalhaven Heads	14.2	34.3	27.88 (1.54)	12	25.8	19.43 (1.24)
Old Man Island	13.02	34.3	27.45 (1.35)	12.3	24.7	19.13 (1.03)
Garlandtown	15.5	36.5	30.61 (1.91)	19.7	25.3	19.71 (0.90)
Quondolo Island	30.3	36.7	34.54 (0.52)	14	26.5	19.81 (0.99)

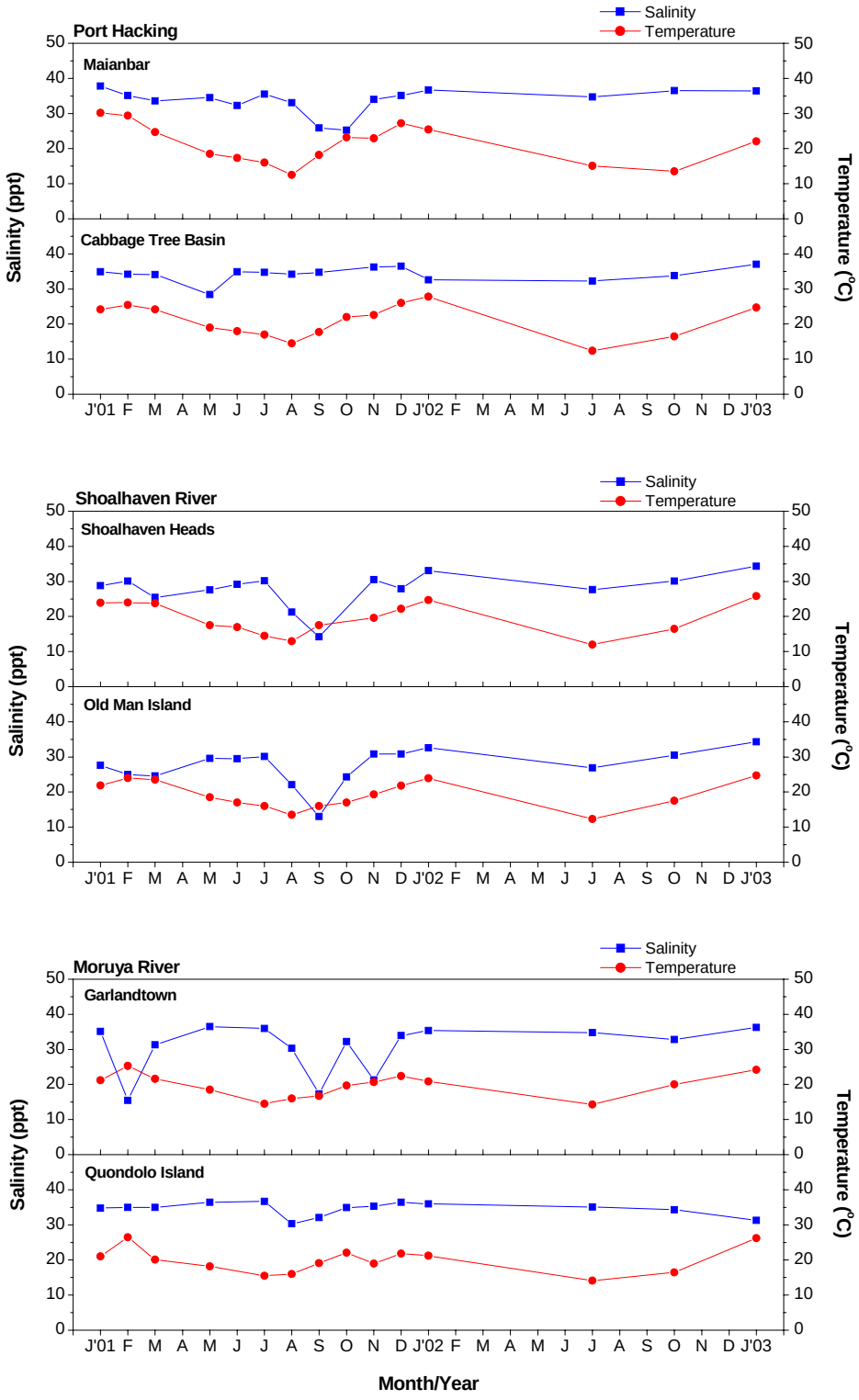


Figure 3.6. Water temperature (degrees Celsius, °C) and salinity (parts per thousand, ppt) measurements at sites within each estuary between January 2001 and January 2003.

3.3.2 Spatial and temporal patterns of abundance

ANOVA for seven important sets of data are summarized in Table 3.3. Patterns of abundance were similar across most sets of data, with relative abundances generally increasing throughout the study period and peaking during the spring and summer months of each year (Figs. 3.7 to 3.13). Significant time x plot interactions in ANOVA across all data sets indicated that differences between plots existed, but that the magnitude of variation differed between times (Table 3.3). As a result, the scale of plots was pooled for abundance graphs and SNK tests revealed consistent patterns of abundance between sites and times within estuaries for most data sets (Figs. 3.7 to 3.13).

The relative abundance of the total number of individuals increased throughout the study period (Fig. 3.7). More individuals were caught from Garlandtown and Old Man Island compared to other sites and no test was available for differences between sites in the ANOVA model. However, SNK tests revealed significant differences between sites in the Shoalhaven and Moruya Rivers' on several occasions. As well, the mean number of burrow openings generally increased throughout the study period (Fig. 3.8) and patterns were similar to the total number of individuals, with a higher number of burrow openings at sites in the Moruya River and at Old Man Island in the Shoalhaven. SNK tests revealed significant differences between sites in the Shoalhaven River on all but two occasions (Jan and May 2001). However, differences between sites in the Moruya River were significant on only one occasion (Oct 2001). Despite similar trends, significant interaction terms in the ANOVA suggested that the number of burrow

Table 3.3. Results of ANOVA testing for differences in the mean number of individuals, burrows, biomass, males, females, recruits and bait-sized individuals of *T. australiensis* between estuaries, sites nested within estuaries, plots nested within sites within estuaries, and between sampling times. All factors considered random. *F*-ratios shown. Significance of *F* test: $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***).

Source of variation	d.f	a) Total Individuals	b) Burrows	c) Biomass	d) Males	e) Females	f) Recruits ≤5mm	g) Bait-sized ≥7mm CL
Estuary	2	0.78	no test	1.37	0.81	0.72	no test	0.27
Site(Estuary)	3	no test	no test	5.74**	no test	no test	no test	no test
Plot(Site, Estuary)	12	16.51***	16.26***	8.30***	10.04***	12.74***	4.76***	9.10***
Time	14	18.29***	1.89	17.27***	11.07***	17.71***	3.69***	15.01***
T x E	28	1.00	2.41**	0.94	0.99	0.75	2.13*	0.96
T x S(E)	42	1.41	1.83**	1.27	1.69*	1.36	2.29***	1.41
T x P(S,E)	168	2.05***	2.85***	1.69***	1.46***	1.62***	1.50***	1.90***
Residual	1080							

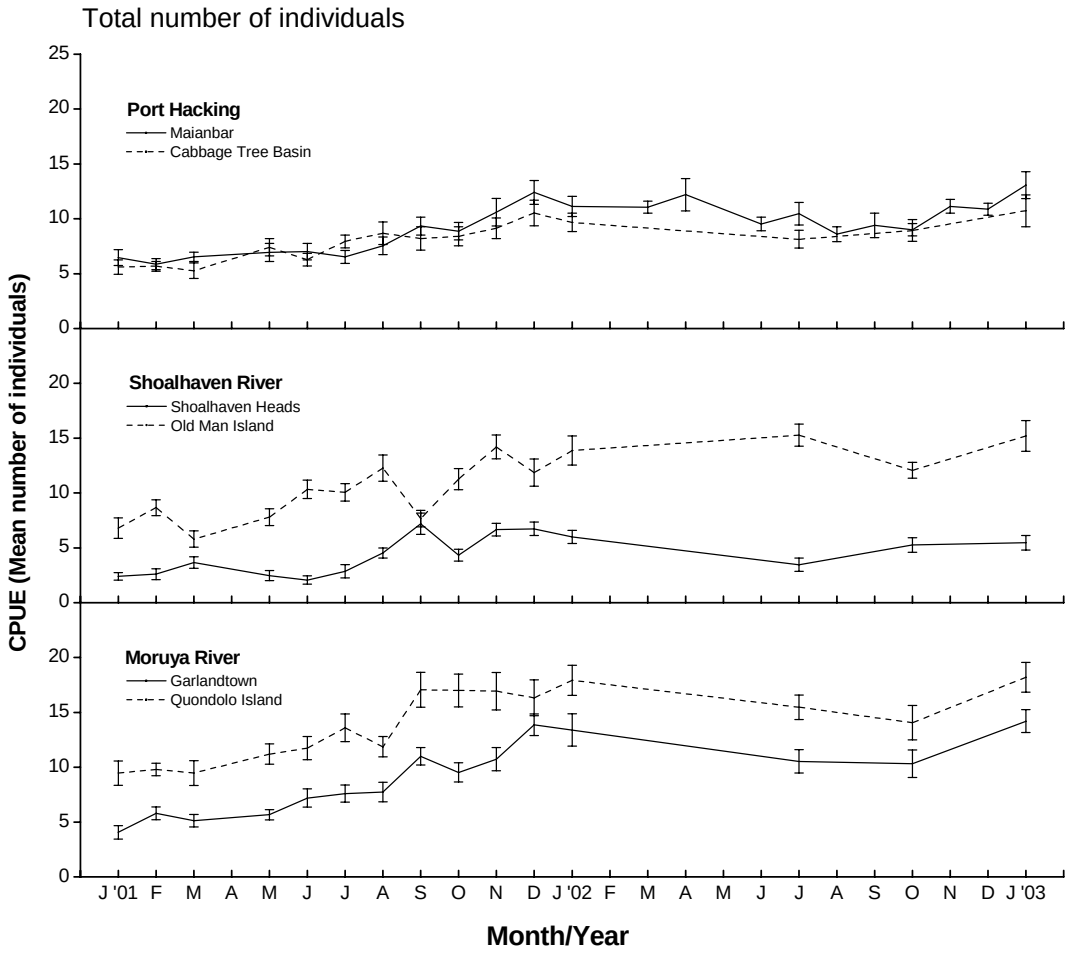


Figure 3.7. Mean (±SE) number of *T. australiensis.* from 5 replicate quadrats, from each of three replicate plots (pooled for each site) for each of two sites within the Port Hacking, Shoalhaven and Moruya Rivers' between January 2001 and January 2003.

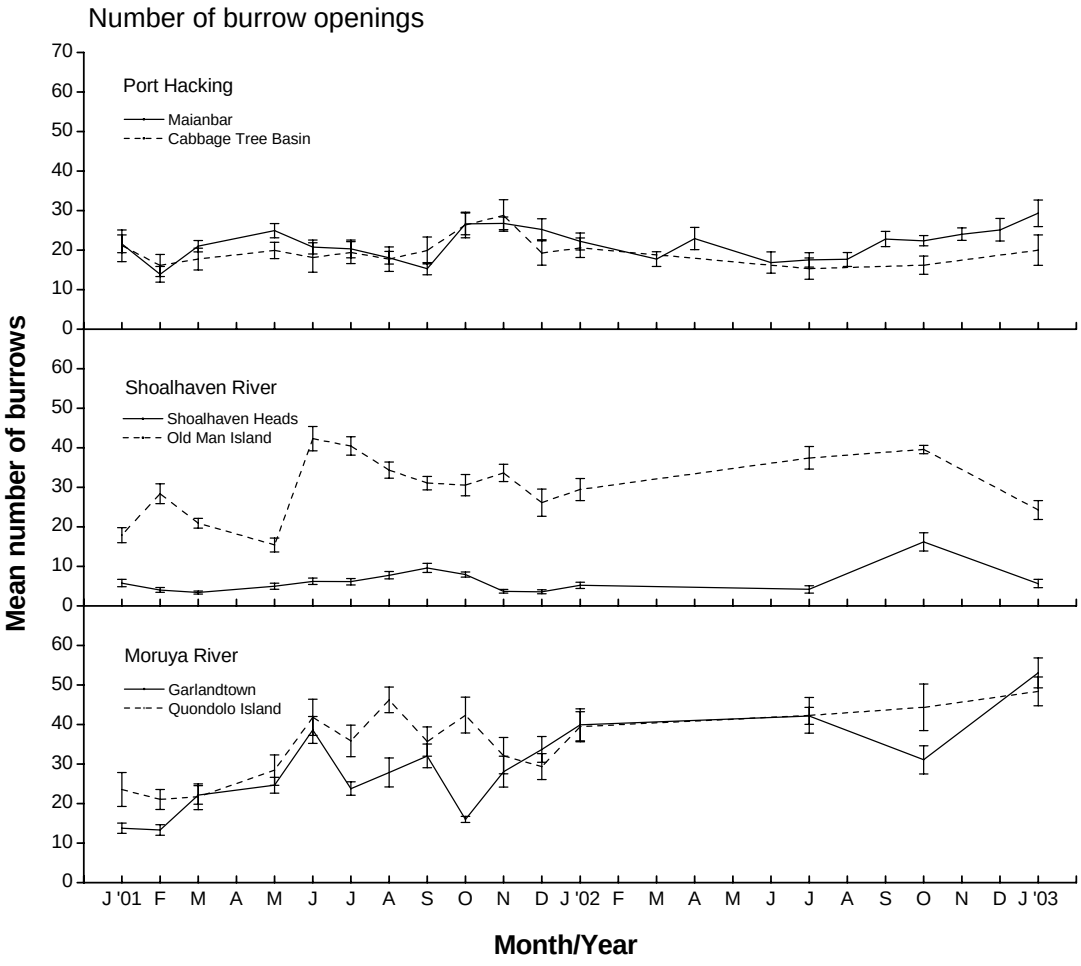


Figure 3.8. Mean (±SE) number burrows of *T. australiensis* from 5 replicate quadrats, from each of three replicate plots (pooled for each site) for each of two sites within the Port Hacking, Shoalhaven and Moruya Rivers' between January 2001 and January 2003.

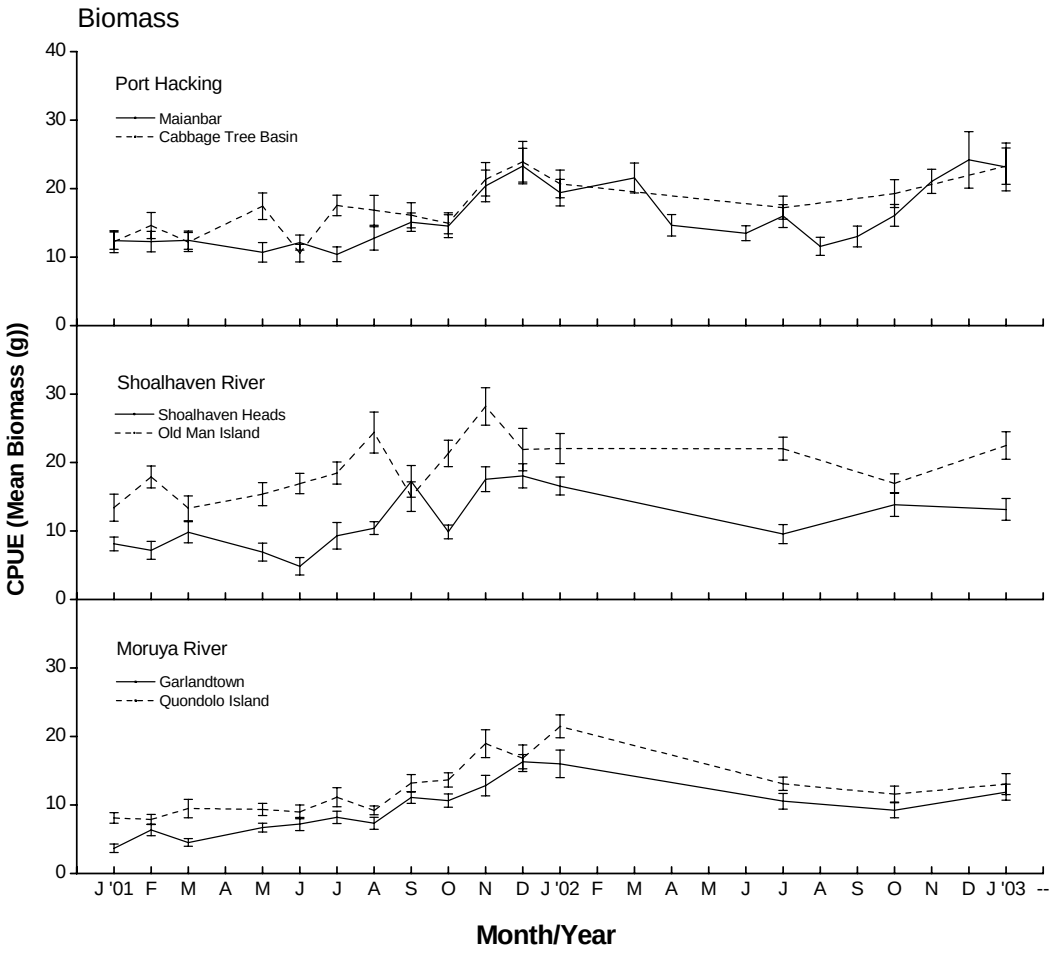


Figure 3.9. Mean (±SE) biomass (g) of *T. australiensis* from 5 replicate quadrats, from each of three replicate plots (pooled for each site) for each of two sites within the Port Hacking, Shoalhaven and Moruya Rivers' between January 2001 and January 2003.

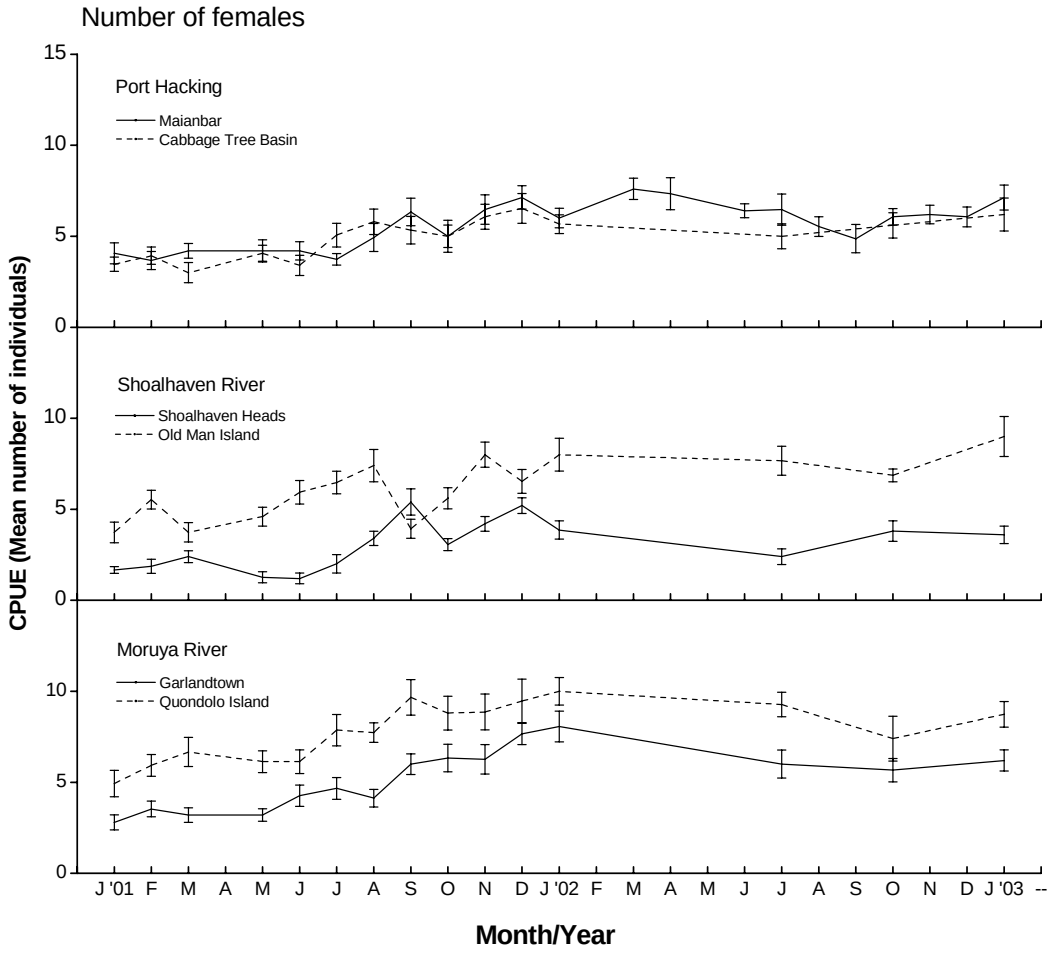


Figure 3.10. Mean (±SE) number of females of *T. australiensis* from 5 replicate quadrats, from each of three replicate plots (pooled for each site) for each of two sites within the Port Hacking, Shoalhaven and Moruya Rivers' between January 2001 and January 2003.

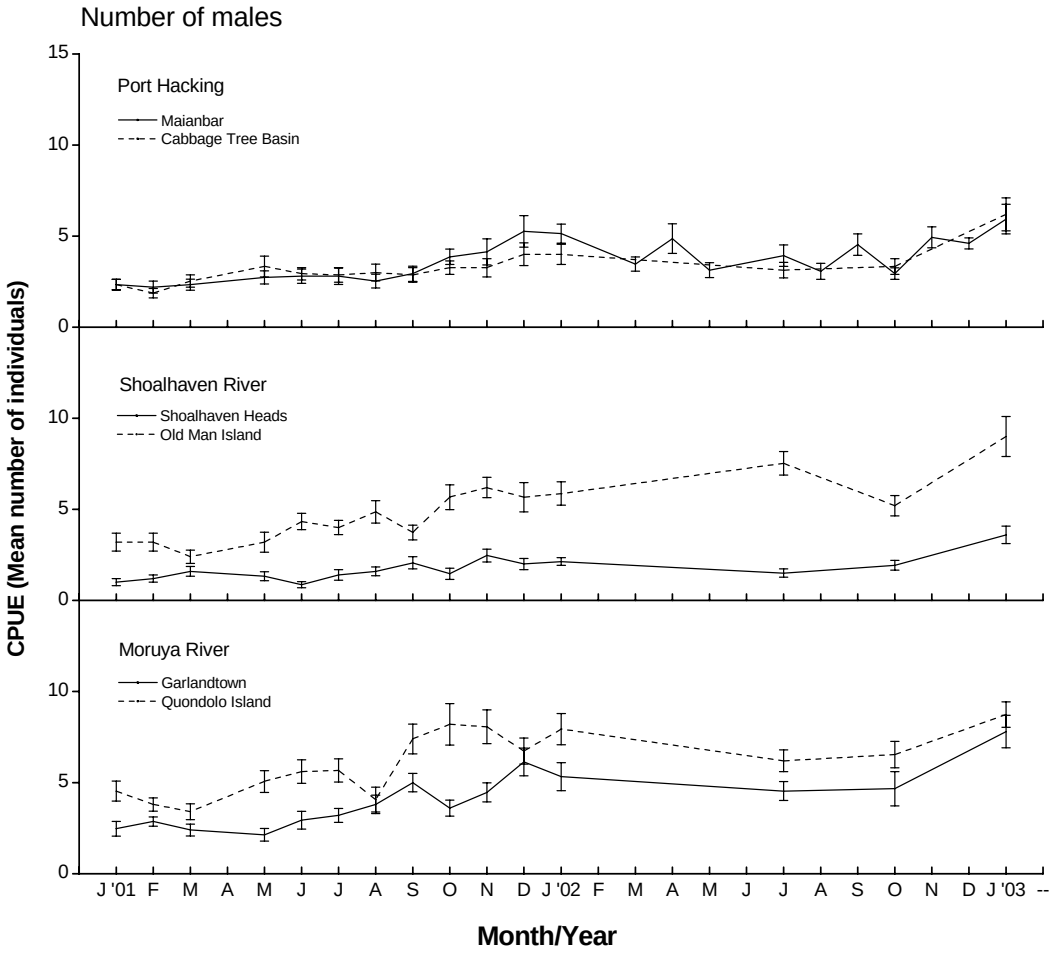


Figure 3.11. Mean (±SE) number of males of *T. australiensis* from 5 replicate quadrats, from each of three replicate plots (pooled for each site) for each of two sites within the Port Hacking, Shoalhaven and Moruya Rivers' between January 2001 and January 2003.

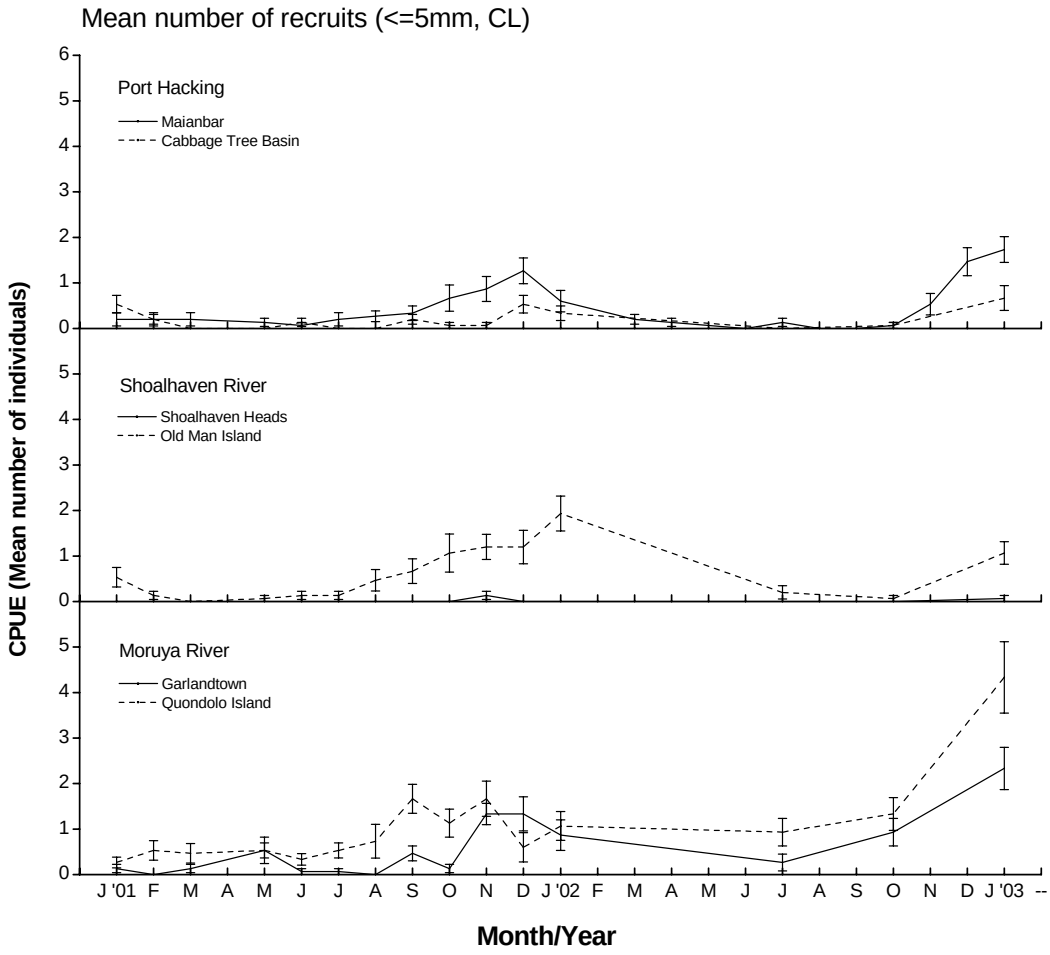


Figure 3.12. Mean (±SE) number of recruits of *T. australiensis* (≤5 mm) from 5 replicate quadrats, from each of three replicate plots (pooled for each site) for each of two sites within the Port Hacking, Shoalhaven and Moruya Rivers' between January 2001 and January 2003.

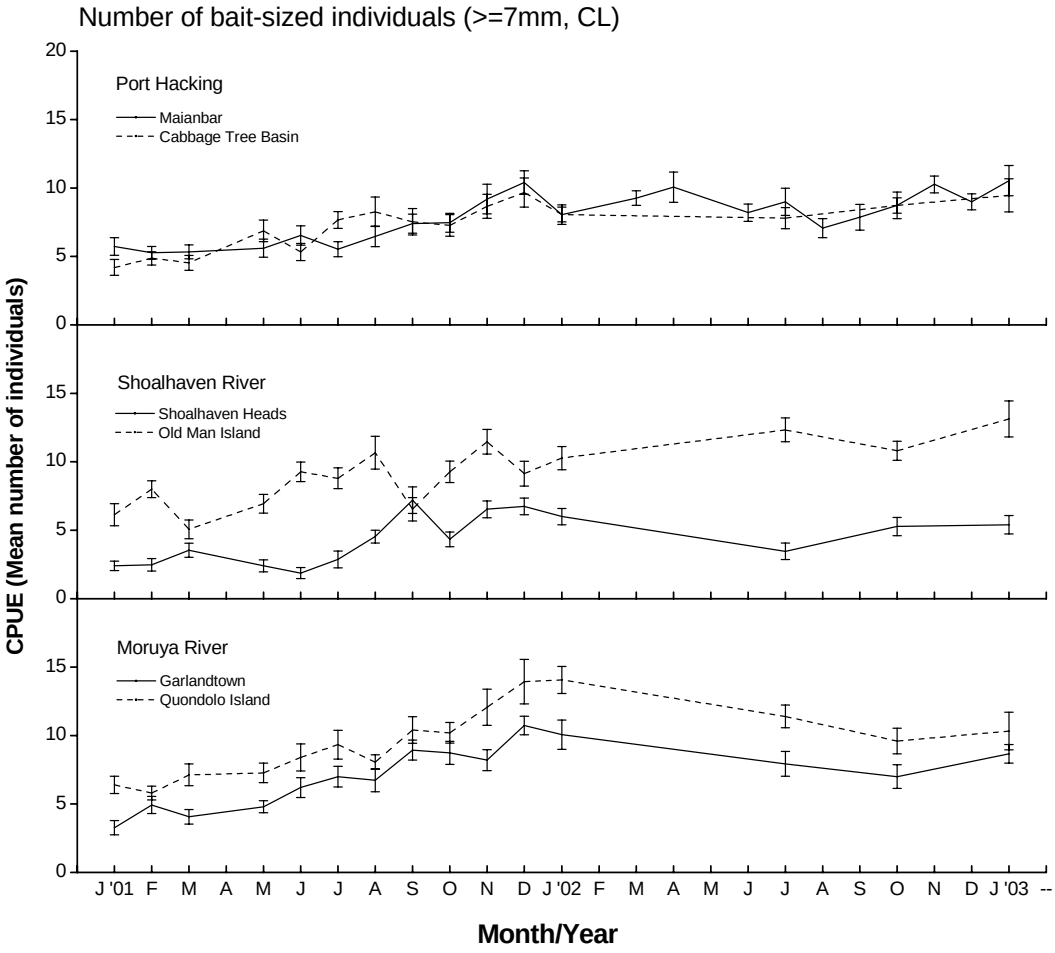


Figure 3.13.. Mean (±SE) number of bait-sized individuals (≥ 7 mm) of *T. australiensis* from 5 replicate quadrats, from each of three replicate plots (pooled for each site) for each of two sites within the Port Hacking, Shoalhaven and Moruya Rivers' between January 2001 and January 2003.

openings was more variable through time and space, than for the total number of sampled individuals.

While total numbers of individuals (Fig. 3.7) and number of burrow openings (Fig. 3.8) were high at sites in Moruya, trends in mean biomass were different (Fig. 3.9). Firstly, mean biomass was actually lower in sites from Moruya River and higher at sites in Port Hacking and the Shoalhaven River. Secondly, despite having the lowest catch rates, mean biomass at Shoalhaven Heads was generally greater or comparable to sites in Moruya throughout the study period. This indicates that despite containing larger numbers of *T. australiensis*, individuals at sites in the Moruya River were smaller than at sites in Port Hacking and Shoalhaven (see also Chapters 4 and 5). ANOVA revealed that the mean biomass of *T. australiensis* differed significantly between sites within estuaries. This trend is evident in Figure 3.9, with SNK tests indicating significant differences in biomass between sites in the Shoalhaven River on most sampling occasions. However, no significant differences were found between sites within Port Hacking and the Moruya River.

Given that populations of *T. australiensis* were female-biased (see Chapter 4), similar trends to the total number of individuals were also found for the number of females (Table 3.3, Fig. 3.10). SNK tests revealed significant differences between sites within Shoalhaven River on most occasions. No significant differences were found between sites in Port Hacking and differences between sites were significant on only one occasion in the Moruya River (Sep 2001). Similar patterns existed for the total number of males, with SNK tests revealing significant

differences between sites in Shoalhaven and Moruya, but not for Port Hacking (Fig. 3.11).

The relative abundance of new recruits of *T. australiensis* was investigated by plotting numbers of individuals ≤5 mm CL (Fig. 3.12). Significant interactions in ANOVA suggested that recruitment was patchy across all of spatial and temporal investigated (Table 3.3). For example, the estimated mean abundance of recruits was higher at sites in the Moruya River and at Old Man Island in the Shoalhaven (Fig. 3.12). Recruitment of individuals to Shoalhaven Heads was very low (total of 2 animals in 2 years) suggesting a local recruitment failure at this site. There also appeared to be a latitudinal gradient in the timing of recruitment, with recruitment occurring earlier in southern estuaries compared to estuaries further north. When January 2001 is compared to January 2002 and 2003, recruitment appeared to get stronger for each of these consecutive years, with very low numbers of recruits in January 2001 across all spatial scales.

For individuals ≥7 mm, which are generally considered to be a suitable size for use as bait (see Chapter 6), relative abundance displayed very similar patterns to the total number of individuals (Table 3.2, Figs. 3.13). Again, more individuals were captured from Old Man Island and Garlandtown, with significant differences between sites within the Shoalhaven and Moruya Rivers', but not in Port Hacking.

3.3.3 Temporal variation in spatial patterns of abundance

Analysis of abundance separately for each sampling time using nested ANOVA allows partitioning of variance components associated with each spatial scale

(estuary, site, plot, and quadrat) to be expressed as the percentage contribution of each scale to overall variation. The analysis was performed separately for each sampling occasion on the total number of individuals, number of recruits and number of individuals ≥7 mm for the first 12 months.

For total number of individuals (Fig. 3.14a), variation between plots increased throughout time, whilst variability between quadrats decreased. This pattern suggests abundances of animals were becoming patchy across sandflats (tens to hundreds of metres) while forming homogenous aggregations at the smaller scale of quadrats (metres). Variability between plots continued to increase throughout time, but variability between quadrats stopped decreasing after October (Fig. 3.14a). This is most likely the result of an increasing patchiness in recruitment at this scale during this time. With recruits removed from the analysis (Fig. 3.14b), variability decreased between quadrats and increased between plots, as in Fig. 3.14a, suggesting that larger or sexually mature animals in the population were still aggregating at small spatial scales (i.e., metres).

For the mean number of new recruits, the quadrat scale explained 50 - 80% of the variability in the model across all sampling times (Fig.3.14c). This indicates that although the abundance of recruits was consistent over the scale of an entire sandflat (hundreds of metres), it was patchy at smaller scales of metres to tens of metres within the sandflat. Similarly, quadrat-scale consistently explained over 50% of the variation for the mean abundance of bait-sized individuals (Fig. 3.14b), with plots accounting for over 20% on most occasions. Thus, abundances of bait-sized individuals were more variable or patchy over small spatial scales

(metres to hundreds of metres) within sandflats, than between sandflats within estuaries and/or between estuaries.

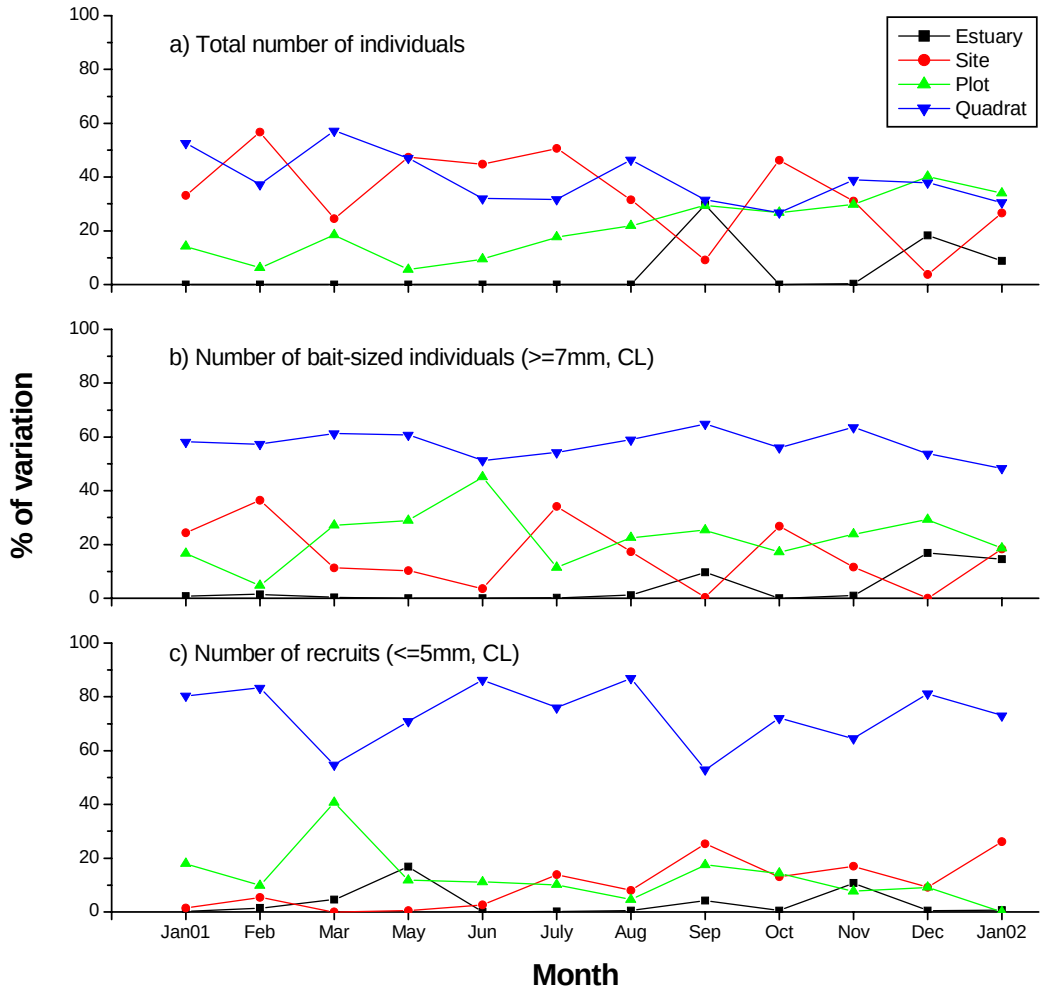


Figure 3.14. Percentage of variation in abundance of *T. australiensis* partitioned between the four spatial scales of the study, derived from nested ANOVA for a) number of individuals b) number of bait-sized individuals (≥7 mm, CL) and c) number of recruits (≤5 mm, CL) Separate nested ANOVA's were completed for each sampling time to examine temporal changes in the spatial pattern of abundance, at each spatial scale.

3.3.4 Temporal patterns of abundance

Since the Maianbar site was sampled approximately monthly for the entire two-year period, it was possible to compare temporal patterns of abundance between years, with respect to the amount of variation within years (i.e., months) and between plots for this site (see Table 3.4). For the mean number of individuals, abundances increased throughout the spring and summer of each year, with abundances decreasing during autumn and winter months (Fig. 3.15). ANOVA revealed significant differences between months within years and between years, with abundances significantly higher in the second year (SNK tests).

For the mean number of burrows, ANOVA revealed a month x plot interaction, which indicated that differences between months occurred, but were not consistent between plots. No significant differences occurred between years. The mean biomass of *T. australiensis* increased throughout spring/summer periods of each year, with lower abundances during autumn/winter months (Fig. 3.15). As a result, significant differences between months were revealed by the ANOVA (Table 3.4). Since the same pattern was consistent between years, no differences were found between years.

The mean number of males and females showed similar patterns of abundance, with significant differences between years and months within years (Fig. 3.15, Table 3.4). SNK tests indicated that abundances were significantly higher in the second year for both males and females. For the mean number of recruits, ANOVA revealed a significant month x plot interaction indicating that differences between months were not consistent across plots. However, no differences were

revealed for years, which suggested that recruitment was consistent between years, even though at the commencement of the study there was an apparent recruitment failure and increasing numbers of recruits in each consecutive year. ANOVA for the relative abundance of bait-sized individuals revealed similar patterns as total abundance, number of males and number of females. There were significant differences between years and months within years, with abundances significantly higher in the second year (Fig. 3.15, Table 3.4).

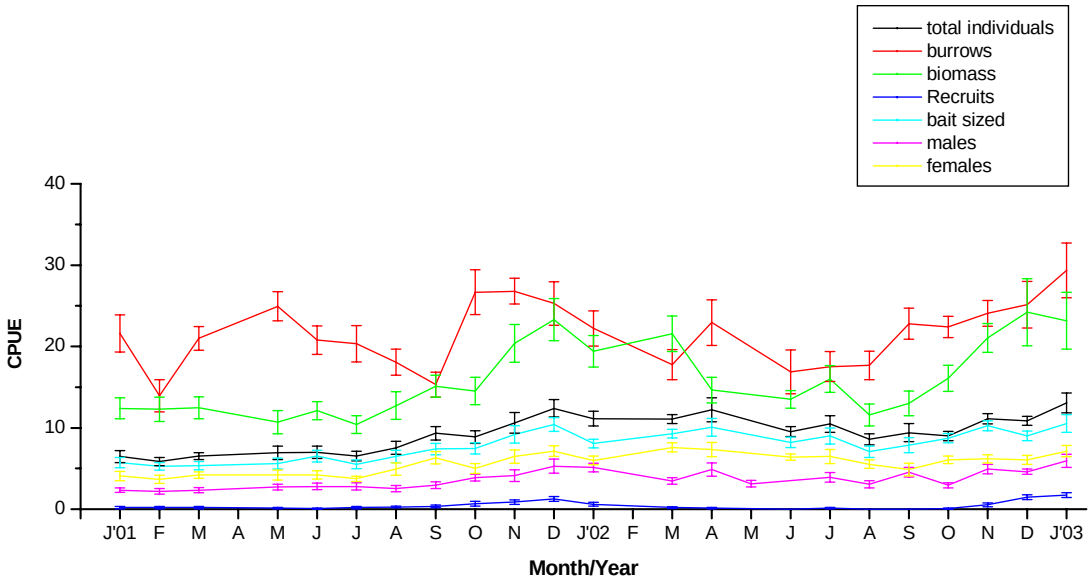


Figure 3.15. Mean (±SE) number of total individuals, burrows, biomass, males, females, recruits (≤ 5mm) and bait-sized (≥ 7mm) individuals of *T. australiensis* from 5 replicate quadrats in each of three replicate plots (pooled) at Maianbar, Port Hacking between January 2001 and January 2003.

Table 3.4. Results of ANOVA testing for differences in the mean number of total individuals, burrows, biomass, males, females, recruits and bait-sized individuals of *T. australiensis* between years, months within years and plots at Maianbar, Port Hacking. All factors considered random. *F*-ratios shown. Significance of *F* test: $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***).

Source of variation	d.f	a) Total Individuals	b) Burrows	c) Biomass	d) Males	e) Females	f) Recruits ≤5mm	g) Bait-sized ≥7mm CL
Year	1	12.05**	0.95	3.76	7.66*	10.88**	0.04	12.02**
Month(Year)	20	3.09**	2.14*	5.70*	2.74**	3.03*	5.14***	3.76**
Plot	2	2.05	6.87	4.06	11.36	1.11	1.56	0.74
Year x Plot	2	1.04	1.88	0.75	0.30	1.69	0.78	0.39
Month(Y) x Plot	40	1.43	1.86**	0.89	1.36	0.89	1.76**	1.04
Residual	264							

3.3.5 Relationship between burrow openings and relative abundance

Counts of burrow openings have often been used to estimate densities of ghost shrimp. In this study, the number of burrow openings was not a reliable predictor of relative abundance of *T. australiensis*. ANCOVA revealed a significant relationship between number of burrows and relative abundance. However, a significant time x location interaction meant that the relationship between burrows and relative abundance was dependent on the particular time and site in question (Table 3.5). Further investigation of regressions between number of burrow openings and number of *T. australiensis* for each site and sampling occasions revealed mostly positive values for slopes of the regression lines, although values were generally small (Table 3.6). Similarly, R^2 values were small, indicating that the proportion of the variation in abundance of *T. australiensis* explained by the number of burrows was generally low. Furthermore, these values differed between sampling times and between sites. Significant positive relationships were more common during spring and summer months and for the Maianbar, Cabbage Tree Basin and Quondolo Island sites.

Table 3.5. Summary of two-factor ANCOVA for the relationship between the number of burrow openings (covariate) and number of *T. australiensis* (dependent variable), between sites (Maianbar, Cabbage Tree Basin, Shoalhaven Heads, Old Man Island, Garlandtown, Quondolo Island) and sampling times (15 sampling occasions from January 2001 - January 2003). (***, $P < 0.001$).

Source	d.f	MS	*F*
Covariate (burrows)	1	4015.035	297.26***
Time	11	271.086	20.07***
Site	5	653.998	48.42***
T x S	55	24.542	1.82***
Residual	1277	13.506	
Total	1350		

Table 3.6. Summary of regressions for the relationship between the number of burrow openings and number of *T. australiensis* at Maianbar (MB), Cabbage Tree Basin (CTB), Shoalhaven Heads (SHH), Old Man Island (OMI), Garlandtown (GT) and Quondolo Island (QI) on each sampling occasion between January 2001 and January 2003. β denotes values for slope of the regression line. R^2 = proportion of the total variance in abundance of *T. australiensis* explained by the number of burrow openings. $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***).

	Site											
	MB		CTB		SHH		OMI		GT		QI	
Month/Year	β	R^2	β	R^2	β	R^2	β	R^2	β	R^2	β	R^2
Jan 2001	0.11	0.12	0.00	0.00	0.10	0.17	0.06	0.01	-0.11	0.05	0.05	0.04
Feb	0.08	0.11	000	0.00	0.22	0.07	0.09	0.10	0.25	0.31*	0.09	0.19
Mar	0.06	0.05	0.06	0.07	0.26	0.07	-0.09	0.06	0.17	0.52**	0.25	0.31*
May	0.07	0.09	0.08	0.06	0.18	0.12	-0.01	0.001	0.05	0.05	0.07	0.10
Jun	0.22	0.39*	0.09	0.34*	0.18	0.18	0.17	0.38*	0.05	0.00	0.08	0.18
Jul	0.06	0.04	0.03	0.02	0.09	0.01	0.02	0.002	-0.13	0.14	0.25	0.62***
Aug	0.10	0.06	0.23	0.18	0.18	0.17	0.12	0.16	-0.04	0.03	0.01	0.008
Sep	0.36	0.74*	0.23	0.56**	0.07	0.01	-0.05	0.01	-0.03	0.02	0.08	0.07
Oct	0.06	0.04	0.03	0.01	-0.20	0.06	0.02	0.008	-0.34	0.25	0.27	0.66***
Nov	0.17	0.10	0.69	0.7***	0.23	0.04	0.02	0.002	0.12	0.22	0.21	0.36*
Dec	0.25	0.50*	0.13	0.21	-0.46	0.15	0.14	0.16	0.15	0.34*	0.28	0.38*
Jan 2002	0.19	0.29*	0.19	0.33*	0.17	0.06	0.21	0.19	0.16	0.26	0.29	0.63***
Jul	-0.05	0.008	0.18	0.36*	0.03	0.002	-0.05	0.02	-0.14	0.08	0.15	0.40*
Oct	-0.14	0.1	0.23	0.29*	0.09	0.10	0.00	0.00	0.06	0.03	0.18	0.45***
Jan 2003	0.05	0.02	0.28	0.56**	-0.26	0.18	0.37	0.40**	0.14	0.28	0.10	0.07

3.3.6 Influence of environmental variables on patterns of abundance

Multiple regressions of environmental variables with abundance of *T. australiensis* were not significant for any site, and low R^2 values indicated that abundance was not correlated with salinity and/or temperature (Table 3.7). Despite this, mean abundances did tend to follow a similar temporal trend to salinity and temperature, increasing during the spring/summer period and decreasing over autumn and winter (see Figs. 3.6 and 3.7), suggesting that these environmental factors may still be important in influencing patterns of ghost shrimp abundance.

Table 3.7. Results of multiple regression analyses of relative abundance of *T. australiensis* against environmental variables of salinity and temperature.

Site	d.f	MS	*F*-ratio	*P*	R^2
Maianbar	2,12	0.126	0.02	>0.05	0.0033
Cabbage Tree Basin	2,11	1.551	0.446	>0.05	0.0750
Shoalhaven Heads	2,11	2.516	0.727	>0.05	0.1169
Old Man Island	2,12	24.814	3.685	>0.05	0.3805
Garlandtown	2,11	1.564	0.003	>0.05	0.0216
Quondolo Island	2,11	0.683	0.062	>0.05	0.0112

3.4 Discussion

This chapter has provided quantitative baseline data on patterns of abundance of *T. australiensis* over a range of spatial and temporal scales for which there was no existing information. Here, variation in the abundance of *T. australiensis* has been described within sandflat locations, between sandflat locations within estuaries and between estuaries in south-eastern NSW, over a two-year period. Temporal variation in abundance has also been investigated and differences in spatial patterns have been examined through time. The spatial scales investigated are particularly relevant to conservation of the bait resource as human impacts are likely to occur at individual sandflat locations within and between estuaries, and therefore would be suitable as potential management units.

The results of the present study indicate significant geographic generalities in the abundance of ghost shrimp, which is uncommon for previous studies documenting natural variations in other marine organisms at a hierarchy of scales (Fairweather, 1991; Kennelly and Underwood, 1992; Ferrell *et al.*, 1993). For example, patterns in abundance were consistent over the largest spatial scale (i.e., between estuaries), but differences between sites within most estuaries existed for several of the data sets throughout the study period. (Figs. 3.7 - 3.13; Table 3.2). Temporal patterns of abundance were consistent across all sites sampled, with relative abundances for all data sets increasing throughout spring and summer periods and decreasing during autumn and winter months. There was also an overall increase in relative abundance throughout the study period. Consistent differences were revealed at the smallest spatial scale (between plots within sites) across all data sets. However, significant time x plot interactions indicated that

although differences between plots existed, the magnitude of these differences varied between sampling times. This result led to the analysis of spatial pattern separately for each sampling time, which showed that as abundances increased across all sites throughout spring and summer, variability between plots (tens to hundreds of metres) also increased and variability between replicate quadrats (metres) decreased (Fig. 3.14). This pattern suggests that populations were forming more homogenous aggregations at small spatial scales within sandflats (metres), which resulted in an increasing patchiness across sandflats (tens to hundreds of metres). Hence, increases in abundances may not have been due to recruitment of new individuals, but rather a redistribution of animals within a sandflat. Although recruitment does partly explain the increases in abundance during spring and summer and indeed the entire study period, the increases in biomass across all sites were larger than would be expected for recruits alone (see Figs. 3.7, 3.9, 3.13). Apparent increases in abundance at Shoalhaven Heads were also observed, even though there were only low levels of recruitment to this site (Fig. 3.13).

Since breeding occurs throughout spring and summer periods for *T. australiensis* (see Chapter 4), the decreasing patchiness at the smallest spatial scale (i.e., metres) may have been the result of animals aggregating to mate (note that this species reproduces sexually and relies on one-on-one encounters). Spawning aggregations have been reported for other marine invertebrates including squid (Hall and Hanlon, 2002; Hanlon *et al.*, 2002; Schoen *et al.*, 2002) and aggregating behaviour has been observed for a number of penaeid prawns (Lucas *et al.*, 1979; Van Zalinge, 1984; Dall *et al.*, 1990; Die and Ellis, 1999). Previous studies have

speculated that *T. australiensis* performs above surface migrations during breeding periods (Hailstone and Stephenson, 1961). Subsurface migrations however seem more likely for this species, given the interconnectivity of burrow galleries and the inherent risk of predation by piscivorous fishes upon shrimp when leaving their burrows. The present study is the first to suggest that some species of thalassinids may migrate within sandflats to form breeding aggregations and highlights the power of the quantitative hierarchical sampling design employed. However, further research is required, perhaps employing greater replication at the scale of plots within sites and over several breeding seasons, before inferring too widely from the present observations.

According to McPhee and Skilleter (2002a), stable population densities with recruitment pulses are apparently common for quantitative studies of thalassinids (see Buchanan, 1963; Tamaki *et al.*, 1997; Berkenbusch and Rowden, 1998). Although Dumbauld *et al.* (1996) reported increasing abundances of the closely related *Neotrypaea californiensis* over a 4-year period in Willapa Bay (Washington, USA). Previous authors have suggested that "neighbourhood stability" is the result of juveniles quickly replacing older or dead individuals through migration and settlement from plankton (Buchanan, 1963; Tunberg, 1986; McPhee and Skilleter, 2002a). However, this apparent stability may simply be an artefact of experimental design in previous investigations (see Table 3.1). Certainly, other studies using indirect burrow counts have found lower densities during winter and have suggested that seasonal declines in burrow density are the result of decreased shrimp activity, due to lower salinities (Posey, 1986; Souza *et al.*, 1998). Salinity was generally lower throughout autumn and winter in the

present study (Fig. 3.6) and burrow densities also declined during these periods (Fig. 3.8). Yet, because the present study also sampled quantitatively in addition to burrow counts, the lower relative abundance of shrimp during autumn and winter periods cannot be explained by reduced activity alone. Multiple regressions revealed no significant relationships between environmental variables, despite the general trends of increasing abundance with increasing salinity and temperatures (Fig. 3.7, Table 3.7). Increases in temperature and salinity during spring and summer, may have initiated the breeding aggregations as suggested above. Increases in temperature have been shown to initiate breeding periods for other decapod crustaceans (Kinne, 1970). If breeding aggregations were to occur then presumably they would not happen whilst the mobility of the animal, imposed by low temperature and salinity, was at its lowest. Hence, increasing temperature and salinity during spring and summer may stimulate *T. australiensis* to aggregate and commence breeding as mobility and burrowing activity increases.

An increase in sampling efficiency is another possible explanation for observed increases in abundances of shrimp during spring/summer periods in the present study (Fig. 3.7). As discussed in Chapter 2, this explanation is unlikely. For example, if increases in efficiency were to occur, they would be expected over the first two or three months of sampling. However, significant increases in CPUE were not observed until after August (Fig. 3.7), at which point more than 7,500 pumps had been completed. Secondly, the mean number of burrow openings also generally increased throughout the first year of the study (Fig. 3.8), although patterns were more variable, perhaps a result of the spatial and temporal variability that exists in the relationship between burrow openings and abundance

of *T. australiensis* (discussed below). It should also be noted that mean abundances of shrimp (and burrow openings) actually decreased during autumn and winter periods of the following year, before once again increasing over spring and summer months in 2002/2003 (Figs. 3.7 and 3.8). This is best illustrated by the Maianbar dataset, as this site was sampled approximately monthly for the entire two-year period.

Recruitment occurred during spring and summer periods across all sites and timing was consistent between years, despite a pattern of earlier recruitment for populations in the south (Moruya River) and stronger recruitment in each consecutive year across all sites. Earlier recruitment to the Moruya River is most likely related to earlier breeding periods, which were observed in this estuary (see Chapter 4). Despite temporal consistency, the results suggest considerable spatial variability in the timing of recruitment. For example, recruitment was patchy within and between sites within estuaries (Fig. 3.13, Table 3.3). Separate analysis of spatial pattern for each time revealed that differences between quadrats accounted for 50 - 80% of variability over the study period (Fig. 3.14). This suggests that recruitment was generally consistent over entire sandflats, but was patchy within sites, particularly at the smallest spatial scales. Differences in abundance of recruits between sites during recruitment periods explained 20 - 30% of variability, which was mostly the result of the marked differences between sites in the Shoalhaven River (Fig. 3.7). For example, only two recruits were captured at Shoalhaven Heads over the entire study period, compared to consistently high levels of recruitment at Old Man Island, just 2 km away (Fig. 3.13). Although it may seem unlikely that the supply of larvae could vary so

dramatically over such a small spatial scale, similar differences in larval recruitment within NSW estuaries have been well documented for some fish species (Worthington *et al.*, 1995).

Selective settlement and post-larval mortality may also affect recruitment of burrowing shrimp to sandflat habitats (Feldman *et al.*, 1997). For example, it is possible that transport of larvae to the Shoalhaven Heads site occurred, but conditions were not favourable for the settlement of larvae. Previous studies of other thalassinid shrimp suggest that juveniles may settle into existing burrows and are tolerated by adults before branching off on their own (Forbes, 1973; Tamaki and Ingole, 1993; Candisani *et al.*, 2001). Studies have also indicated the presence of adults might have a positive effect on recruitment success. For example, Tamaki and Ingole (1993) found that larvae of *C. japonica* settling outside of adult populations, did not survive until the next breeding season and speculated that sediments already reworked by adults may be softer and facilitate faster burrowing by settling larvae and juveniles. Feldman *et al.* (1997) found the ghost shrimp *N. californiensis* preferred substrate that contained mud compared to epibenthic shell. Strasser and Felder (1999) demonstrated that individuals of *Callichirus major* from the Atlantic coast required water previously conditioned by the presence of adults and sand before settling in laboratory experiments.

Relative abundance of shrimp and burrow density was lower at Shoalhaven Heads (Figs. 3.7 to 3.8) compared to Old Man Island and other sites in the study, which given the results of the above studies, may have had consequences for settlement and recruitment of juveniles. Firstly, the lower numbers of shrimp may not have

effectively conditioned the surrounding water to promote large numbers of larvae to settle. Secondly, upon settlement larvae may not have been able to seek existing burrows in which to settle, leaving them open to predation by fishes and/or desiccation at low-tide. Thirdly, lower re-working of sediments by adult shrimp at this site due to lower abundances may result in a harder substrate, thereby inhibiting burrowing by settling larvae and juveniles, leaving them at risk of predation by demersal fishes and epibenthic predators such as crabs, and low-tide desiccation. Clearly, there is much scope for further research into factors controlling such distinct differences in the abundance of new recruits between relatively close sites within an estuary. A starting point may involve conducting plankton tows during recruitment times to validate whether or not larvae are actually being transported to the site, before investigating the roles of selective, differential settlement and post-settlement mortality.

The low numbers of shrimp and absence of recruits at Shoalhaven Heads is of concern, as this site is easily accessible and a popular harvesting location. Also, the variability in recruitment strength between years across all sites, although not uncommon for marine invertebrates (Caffey, 1985) should be noted. For example, in the first summer of the study (Jan - Feb 2001) recruitment was very low across a large geographic range, suggesting that unfavourable large-scale oceanic processes may have been operating, as shrimp larvae are planktonic and are transported out of estuaries into adjacent oceanic waters by tidal processes. In fact, recruitment generally increased in each consecutive year of the study and was highest on the final sampling occasions at most sites. Throughout the entire duration of the study, the region was experiencing a severe drought, caused by an

El-Nino event (Anon, 2004a). This may have led to increased survival of larvae within estuaries due to an absence of large fluctuations in salinity, which have been found to be deleterious to the survival of shrimp larvae (Forbes, 1978; Thessalou-Legaki, 1990). Anecdotal evidence for the Moruya River suggests that abundances of adult shrimp decline considerably during flood events. Hence, sampling over longer temporal periods and wetter years (i.e., La-Nina phase) would provide interesting comparisons of abundance and recruitment patterns.

The use of catch per unit effort to estimate abundance is uncommon for species of burrowing shrimp (see McPhee and Skilleter, 2002a), but has been used extensively in studies of other crustaceans, particularly those of commercial importance (Kennelly, 1992). This makes comparisons with studies that have used density estimates, including coring or burrow counts, difficult. The present study counted burrow openings within quadrats prior to pumping and found that the relationship between burrow openings and abundance, whilst significant on some occasions, also varied significantly (and inconsistently) through time and space. A similar finding in Moreton Bay (Qld) (McPhee and Skilleter, 2002a) prompted the authors to conclude that counts of burrow openings were an unreliable estimate of population size.

In the present study, burrow densities within individual quadrats ranged from zero to 770 m^{-2}, with mean values ranging from 60 (±49.1) m^{-2} to 326 (±190.7) m^{-2}. Hailstone and Stephenson (1961) reported burrow densities of up to 500 m^{-2} in Moreton Bay, whilst McPhee and Skilleter (2002a) also sampling in Moreton Bay suggested that these densities may be exception rather than the rule, with mean

densities of up to approximately 20 m^{-2}. Whilst the present results are some of the highest burrow densities reported for *T. australiensis*, they are similar to the results of Hailstone and Stephenson (1961) and other studies of thalassinidean shrimps where burrow densities commonly range between 100 and 500 m^{-2} (Posey, 1986; Cockroft and Tomalin, 1987; Hanekom *et al.*, 1988; Wynberg and Branch, 1991).

Further difficulties in using CPUE estimates arise when attempting to determine standing stock sizes and biomass for particular locations, especially for benthic organisms. The present study can provide some information on the magnitude of stock sizes for *T. australiensis* in south-eastern NSW. Assuming that the yabby pump sampled all individuals within a 0.1 m^2 area, and averaging for the entire study period, allows the mean number of shrimp per m^2 for each location to be calculated (Table 3.8). The area of each sampling location has been calculated using aerial photographs and GPS mapping. Multiplying the size of the sampling site by the average number of shrimp per m^2 gives coarse estimates of stock sizes and total biomass for each site (Table 3.8). Note that it may be argued that the yabby pump overestimates numbers by dragging in individuals from outside the quadrat, due to the interconnectivity of burrows, or underestimates numbers by not completely sampling a quadrat. Nevertheless, the results reported for these NSW estuaries indicate that standing stock sizes at individual sites are in the order of millions of individuals.

Table 3.8. Table showing mean (±SE) burrow density (m^{-2}), shrimp density (m^{-2}) and biomass (m^{-2}) of *T. australiensis* for each site over the entire study period and estimates of the magnitude of stock sizes and stock biomass (see text for details).

Site	Burrow density (m^{-2})	Shrimp density (m^{-2})	Biomass (g) (m^{-2})	Site area (m^{-2})	Estimated stock size (No. of individuals)	Estimated stock biomass (kg)
Maianbar	207.1 (±96.7)	92.9 (±38.5)	160.4 (±86.4)	169,361.38	15,733,672 (±6,520,413)	27,166 (±14,633)
Cabbage Tree Basin	183.4 (±12.5)	80.3 (±37.6)	173.7 (±82.5)	25,327.41	2,033,791 (±825,673)	4,399 (±2,089)
Shoalhaven Heads	60 (±49.1)	43.8 (±27.7)	120.1 (±68.2)	58,684.70	2,570,390 (±1,625,566)	7,048 (±4,002)
Old Man Island	284 (±135.3)	108.7 (±47.5)	194 (±87.8)	27,170.12	2,953,392 (±1,290,581)	5,271 (±2,385)
Garlandtown	272.8 (±164)	91.2 (±46.84)	95.4 (±54.2)	48,624.30	4,434,536 (±2,277,562)	4,639 (±2,635)
Quondolo Island	326.3 (±190.7)	140 (±57.6)	124.5 (±61.9)	24,623.97	3,447,356 (±1,418,341)	3,066 (±1524)

The results of the present study indicate that abundances of *T. australiensi*s were generally more variable on smaller spatial scales such as between sites within estuaries (1 – 2 km) and within sites (tens to hundreds of m), than across large spatial scales such as between estuaries (hundreds of km). These spatial patterns also varied through time, suggesting that *T. australiensis* may form spawning aggregations prior to and during breeding periods. Increases in abundances over longer temporal scales (i.e., between years) appear to be the result of recruitment, which generally increased during each consecutive year of the study. On smaller spatial scales, such as between sandflats within estuaries and within sandflats, recruitment was patchy indicating that transport of larvae, selective settlement and post-larval mortality may be important factors in determining recruitment for this species. Over large spatial scales (between estuaries), recruitment was less variable, which probably reflects the success of the wide dispersal strategy of *T. australiensis* in eastern Australia. The present results are discussed in relation to the life-history and management of *T. australiensis* in NSW in a later chapter (Chapter 7), where directions for further research are also outlined.

Chapter 4

Reproductive biology of *Trypaea australiensis* in south-eastern Australia

4.1 Introduction

Knowledge of the reproductive biology of harvested organisms underlies traditional fisheries management strategies, which aim to ensure optimal harvesting and sustainability of resources (Hilborn and Walters, 1992). For commercially and recreationally important finfish and crustaceans, scientific information on life-history parameters including size at maturity, sex ratio, reproductive periodicity and size-specific fecundity are fundamental to stock assessment procedures and consideration of management strategies such as size restrictions, seasonal closures and bans on collection of reproductive females (Kennelly and Watkins, 1994). Similarly, such information is also necessary for ecosystem approaches to management, such as the inclusion of stocks in Marine Protected Areas (MPA's) and sanctuaries, to provide refuges for breeding populations (Smith and Pollard, 1996).

Marine invertebrates display a wide range of reproductive tactics in their life histories (Stearns, 1976). For example, species may reproduce sexually and/or asexually and be either dioecious, with separate sexes that do not change within their life-cycle, or hermaphroditic, where individuals function either simultaneously or sequentially as both males and females. However, most economically important decapod crustaceans such as crabs, penaeid prawns, and lobsters are dioecious and reproduce sexually, with males transferring spermatophores to females, which are then stored for varying lengths of time

depending on the species (King, 1995). During spawning, eggs are released from the ovaries of females and are fertilised as they pass over the spermatophores. Some species, such as penaeid prawns release fertilised eggs directly into the water column (Dall *et al.*, 1990), whereas the majority of decapod crustaceans carry eggs beneath the abdomen where they are incubated before hatching into larvae.

Whilst decapod crustaceans display considerable inter-specific variation in reproductive characteristics, there also exists significant intra-specific variability, which makes management of harvested stocks difficult. For example, within populations, fecundity often increases linearly with female carapace length (Morgan, 1972; Hines, 1982; Kennelly and Watkins, 1994; Stewart and Kennelly, 1997) and environmental variables such as temperature, photoperiod, food availability and habitat may influence the commencement and duration of breeding seasons (Cobo and Fransozo, 2003). Also, these factors have been shown to be important in determining size at maturity, fecundity, and egg size, which may result in latitudinal clines between geographically separated populations (Jones and Simons, 1983; Lardies and Wehrtmann, 2001). Furthermore, the reproductive output of decapod crustaceans can vary temporally, both within and between reproductive periods (Kennelly and Watkins, 1994). Hence, studies seeking to determine the reproductive biology of harvested species for stock assessment and management should ensure populations are sampled over appropriate spatial and temporal scales and include a wide size range of individuals (Kennelly and Watkins, 1994).

Burrowing thalassinid shrimps are sexually reproducing, dioecious decapod crustaceans, however descriptions of mating are uncommon and the nature of copulations poorly understood. A number of studies have investigated various aspects of thalassinid shrimp reproductive biology (Table 4.1). However, they are relatively few when compared to similar studies of other decapod crustaceans, particularly those captured commercially. Nevertheless, like other decapods, the reproductive characteristics of thalassinidean shrimp show considerable inter- and intra-specific variation. For example, whilst female-biased sex ratios are common for thalassinids (Tunberg, 1986; Vaugelas *et al.*, 1986; Felder and Lovett, 1989; Hanekom and Baird, 1992; Dumbauld *et al.*, 1996; Tamaki *et al.*, 1997; Pezzuto, 1998; Souza *et al.*, 1998) both male-biased (Rowden and Jones, 1994) and equal ratios (Dworschak, 1988), have been reported for different size classes. Temporal differences in sex ratios may also exist within populations (Berkenbusch and Rowden, 1998; Pezzuto, 1998). Furthermore, despite many species breeding during warmer months, ovigerous females of various species have been reported throughout all months of the year (Table 4.1), and differences in the timing and duration of breeding periods have been observed for the same species in different areas or regions (Berkenbusch and Rowden, 2000). Also, populations may display either unimodal or bimodal peaks in reproductive activity. For example, *Callianassa subterranea* (Rowden and Jones, 1994) and *C. japonica* (Tamaki *et al.*, 1997) have major and minor peaks in breeding activity, which results in extended breeding seasons, whereas *C. filholi* (Berkenbusch and Rowden, 1998) and *Callichirus major* (Souza *et al.*, 1998) have single peaks in the percentage of ovigerous females and shorter breeding periods.

Table 4.1. Reproductive characters of various burrowing thalassinid shrimp (table based on and modified after Dworschak (1988) and Pezzuto (1998)). ED = egg diameter; I = incubation period; CL = carapace length of ovigerous females; TL = total length of ovigerous females; stages = number of larval stages (L = larval; PL = post-larval); LD = duration of larval development in day; LH = life habit of larvae (p = planktonic; b = benthic). * = *vide* Dworschak (1988) and/or Pezzuto (1998). References: (1) Andryszak, 1986; (2) Aste and Retamal, 1983*; (3) Berkenbush and Rowden, 1998, (4) Berkenbush and Rowden, 2000; (5) Cano, 1891*; (6) Souza *et al.*, 1998; (7) Vaugelas *et al.*, 1986; (8) Devine, 1966; (9) Dworschak, 1988 (10) Dworschak and Pervesler, 1988; (11) Dumbauld *et al.*, 1996; (12) Felder and Rodrigues, 1993; (13) Forbes, 1973; (14) Forbes, 1977b; (15) Gurney, 1937*; (16) Hailstone and Stephenson, (1961); (17) Hill, 1977; (18) Kenway, (1981); (19) Kinoshita *et al.*, 2003; (20) Konishi *et al.*, 1990*, (21) Kurata, 1962*; (22) Lutze, 1938*; (23) Nates *et al.*, 1997; (24Ngoc-Ho, 1977; (25) Nurse (1980); (26) Pearse, 1945; (27) Pezzuto, 1998; (28) Pohl, 1946; (29) Robertson, 1977; (30) Rodrigues, 1976*; (31) Rowden and Jones, 1994; (32) Samuelsen, 1974*; (33) Sandifer, 1973*; (34) Sankolli and Shenoy, 1975*; (35) Santos and Paula, 2003; (36) Shenoy, 1967*; (37) Tamaki *et al*., 1996; (38) Tamaki *et al*., 1997; (39) Thessalou-Legaki, 1990; (40) Thessalou-Legaki and Kiortsis, 1997; (41) Tunberg, 1986; (42) Webb, 1919*.

Species	Breeding	Breeding	No. eggs/female	ED	I	CL	TL	Stages	LD	LH	Reference/s
Callianassa. bouvieri			80	800			18-25				10
C. filholi	Jun-Jan	spr/sum	498-11296 (n=113)	370-470	5.5 wk	5.6-16	34-54	5L, 1PL	150	P	8, 3, 4
C. japonica	Jun-Oct	sum/aut	962 max (n=289)	500-600	13-22 d		34-54	6L, 1PL	20-25	P	37, 38
C. kewalamanii				700-900				2L, 2PL	7-9	p	34*
C. kraussi	May-Jan	aut/win	12-193	900-1800	32.5 d	6-11		2L	3-5	B	13, 14
C. petalura								6L, 1PL	15-16	p	20*
C. subterranea		sum	7000	500-600	30 d		47	4L, 1PL	35	p	22*, 31
C. tyrrhena			56-1128 (n =59)	1180				2L, 1PL	3.2	p	39, 40
Callichirus garthi								5L, 1PL	48	p	2*
C. major	Nov-Jan		600-8200	875-1020	>32d		136	3L	14	p	28, 30*, 6
C. armatus				850-1050	19.5 d		100			p	7
Lepidophthalmus louisianensis			598	900-1200	≤25-30 d	17		2L, 1PL	3-4	p	12, 23
L.sinuensis			258			10-13		2L, 1PL	3-4	p	23
Neotrypaea californiensis	Apr-Aug	spr/sum	200-14000 (n=44)	620-830	4-5 wk	9-19	41-88	5L, 1PL	42-56	p	11
N. uncinata								5			2
Sergio mirim	Sep-Jan	spr/sum	300-6600 (n=12)	1080-1170		18-27	64-98	2L, 1PL	7-14	p	27

Table 4.1 Continued

Trypaea australiensis	Mar-Nov	aut/spr			6-7 wk	9-12		6L, 1PL	120-160		16
	Sep-Feb	Ear. sum									29
	May-Oct	aut/spr	93-2236 (n=5)								18
	Feb-Oct	late sum-spr	4134-8126 (n=10)	680x590	40	9.36-14.96	43-75	2L, 5PL	-	p	25
Upogebia affinis			10,000	450			47-75	4L, 1PL		p	26*, 33*, 1
U. africana			300-2000	450	52 d	12-20				p	17
U. danai								4L, 1PL		p	15*
U. darwini				1000			31	2L, 1PL	5	p	24
U. deltaura	May-Aug	spr/sum	4757 (n=4)	500-558		14	40	4L, 2PL	30-60	p	41, 7; 32*
U. kempi								4L, 2PL	22	p	36*
U. major	Dec-May	win/spr	5899-11718 (n=39)	780-920	30d	25.1-34.4		3L	30	p	21*, 20*,
U. pugettensis	Oct-May		200-12000 (n=35)	730-850		20-30					11
U. pusilla	Mar-Sep		400-12000 (n=98)	400-490	35.5d	8-19	36-60	4L, 1PL	35	p	5*, 9, 35
U. savignyi			1000				35	1L		B	15
U. stellata				500		18	53	4L, 2PL		p	32*, 42*

Intra-specific differences in fecundity within populations have been reported for some species of burrowing shrimp. Number of eggs per brood is often related to female size (Hill, 1977; Dworschak, 1988; Hanekom and Erasmus, 1989; Thessalou-Legaki and Kiortsis, 1997; Berkenbusch and Rowden, 2000). For some species, fecundity increases with size to a point before decreasing in the largest animals (Forbes, 1977a), while in other species no correlations between female size and fecundity exist (Buchanan, 1963; Kinoshita *et al.*, 2003). In addition to female size, fecundity may also be dependent on egg size and number of larval stages, as high egg numbers and small egg size often result in extended planktonic development, whilst larger egg size and lower fecundity are frequently associated with an abbreviated larval development (Table 4.1). Despite the above relationships, previous studies on the relationship between female size and fecundity are few and have often used only a small number of animals to estimate egg counts and other measurements (Table 4.1).

As with previous accounts of shrimp abundance (see Chapter 3), studies of thalassinid reproductive biology have generally been conducted over restricted spatial and temporal scales such as single sites, estuaries, times and seasons. Hence, intra-specific differences in the reproductive biology of burrowing shrimp between different populations have not been well documented. Hill (1977) compared the breeding biology of *Upogebia africana* from 3 estuaries in South Africa. However, samples from each estuary were taken during different breeding seasons, with as many as 10 years between collections from different estuaries. Furthermore, sampling methods were not quantitative and comparisons were made between data collected with different sampling methods. *U. pusilla*, from

the northern Adriatic Sea in the Mediterranean, displays variation in the timing and duration of breeding periods, the proportion of ovigerous females, and female size at maturity and fecundity (Dworschak, 1988).

Perhaps the most comprehensive study investigating intra-specific variation in the reproductive biology of burrowing shrimp comes from Berkenbusch and Rowden (2000), who sampled populations of *C. filholi* throughout its entire range in New Zealand. In this study, size at maturity, timing of breeding and fecundity all differed significantly between populations. As well, embryo size increased significantly with latitude. Despite the considerable spatial replication in this New Zealand study, populations were only sampled intermittently throughout a single breeding season. No single study has yet considered the reproductive biology of any thalassinid species simultaneously over multiple spatial and temporal scales and across a wide geographic range. Such comparative studies have been conducted for other marine decapods and can provide an important basis for theoretical considerations of life-history strategies (Hines, 1982; Clarke, 1987) and assessment and management of harvested stocks (Morizur *et al.*, 1981).

In Australia, few studies have investigated the reproductive biology of *T. australiensis* (Table 4.1). Nevertheless, they have been conducted in different regions throughout the range of the species and together, suggest intra-specific variability in reproductive characteristics. For example, the commencement and duration of breeding period differs between all studies and appears to be related to latitude, with populations further south appearing to commence breeding progressively earlier than northern populations (Table 4.1). Hailstone and

Stephenson (1961) compared three populations approximately 5 to 20 km apart in Moreton Bay in Queensland over a 20-month period and found minor differences in size of female size at maturity between sites. Similarly, Kenway (1981) found differences in female size at maturity between populations in three different estuaries separated by 10 to 40 km in the Townsville region in northern Queensland. However, only a single site was sampled in each estuary, making comparisons between estuaries somewhat inconclusive. The relationship between latitude and breeding needs to be tested concurrently over a number of spatial and temporal scales.

Of the few studies that have investigated reproductive characteristics of *T. australiensis*, only two have examined aspects of reproductive output such as fecundity and egg size (Nurse, 1980; Kenway, 1981). These studies counted and measured eggs from only a small number of individuals ($n \leq 10$) and over a relatively narrow size range, which contained mostly larger individuals from single sites. Nevertheless, they suggest high fecundity and a relatively small egg size compared to other burrowing shrimp species. Furthermore, previous studies of embryonic development and larval biology also suggest a strategy of high fecundity and small egg size, followed by a long larval period with more than 5 stages. For example, Dakin and Colefax (1940) described 6 larval stages, whereas a later study by Nurse (1980) described 7 stages. However, neither study provides information on the development time of larvae, despite comprehensive descriptions of larval stages and a detailed account of reproductive and alimentary anatomy, and embryonic development by Nurse (1980). Hailstone and Stephenson (1961) inferred a larval period of around 5 to 6 months from plankton samples

collected a month after ovigerous females appeared in populations and presence of post-larvae in adult populations. However, no study has successfully reared *T. australiensis* larvae under laboratory conditions past stage 2, which is perhaps due to the longer development time compared to other species.

The lack of information on the reproductive biology of *T. australiensis* in NSW, combined with the intra-specific variability observed in previous studies in Australia, and indeed for other species of burrowing thalassinid shrimp, makes stock assessment and management difficult. For example, enforcing closures or restrictions on the collection of ovigerous females during reproductive periods or recruitment events may not be appropriate across an entire state, if latitudinal differences exist across large geographic scales. Similarly, potential differences in female size at maturity and fecundity between populations would make implementation of strategies such as minimum size limits difficult. Furthermore, differences in reproductive biology may exist between sites within estuaries. For example, previous studies have found that populations of burrowing shrimp closer to the entrance of an estuary, extruded eggs earlier than populations further upstream (Forbes, 1978; Dumbauld *et al.*, 1996).

This chapter provides new baseline information on various aspects of the reproductive biology of *T. australiensis*, over a range of spatial and temporal scales relevant to stock assessment and management, and across a large regional area of south-eastern NSW where previous investigations have been limited.

4.2 Materials and methods

4.2.1 Collection of samples

In order to investigate spatial and temporal patterns in the reproductive biology of *T. australiensis*, samples were collected as part of the main sampling program described in Chapter 3. In the laboratory, additional observations related to reproduction included the macroscopic appearance of the female ovaries through the semi-transparent exoskeleton which were either; white or transparent (stage 1), yellow (stage 2), yellow/orange (stage 3), orange (stage 4) or crimson (stage 5) (stages modified after Hailstone and Stephenson, 1961). Females carrying eggs (i.e., ovigerous females) were recorded and embryos were classified as either uneyed or eyed (presence of eyespots and/or eyespots and tails). Previous studies of *T. australiensis* (Hailstone and Stephenson, 1961), have classified the chronological development of embryos as being orange without eyespots for freshly extruded eggs, then yellow without eyespots and then yellow with eyespots. In the present study, both orange and yellow eggs were found to possess eyespots under a dissecting microscope (Plate 4.1), whereas Hailstone and Stephenson (1961) examined eggs macroscopically in the field. Hence, the use of the eyed/uneyed method rather than colour change was used to follow egg development. Condition of testes and vasa deferentia were not determined for males. Instead, male maturity was determined through linear regressions of carapace length (CL) and chela height (ChH) using REGRANS (Pezzuto, 1993) and is considered in a later chapter of this thesis (Chapter 5).

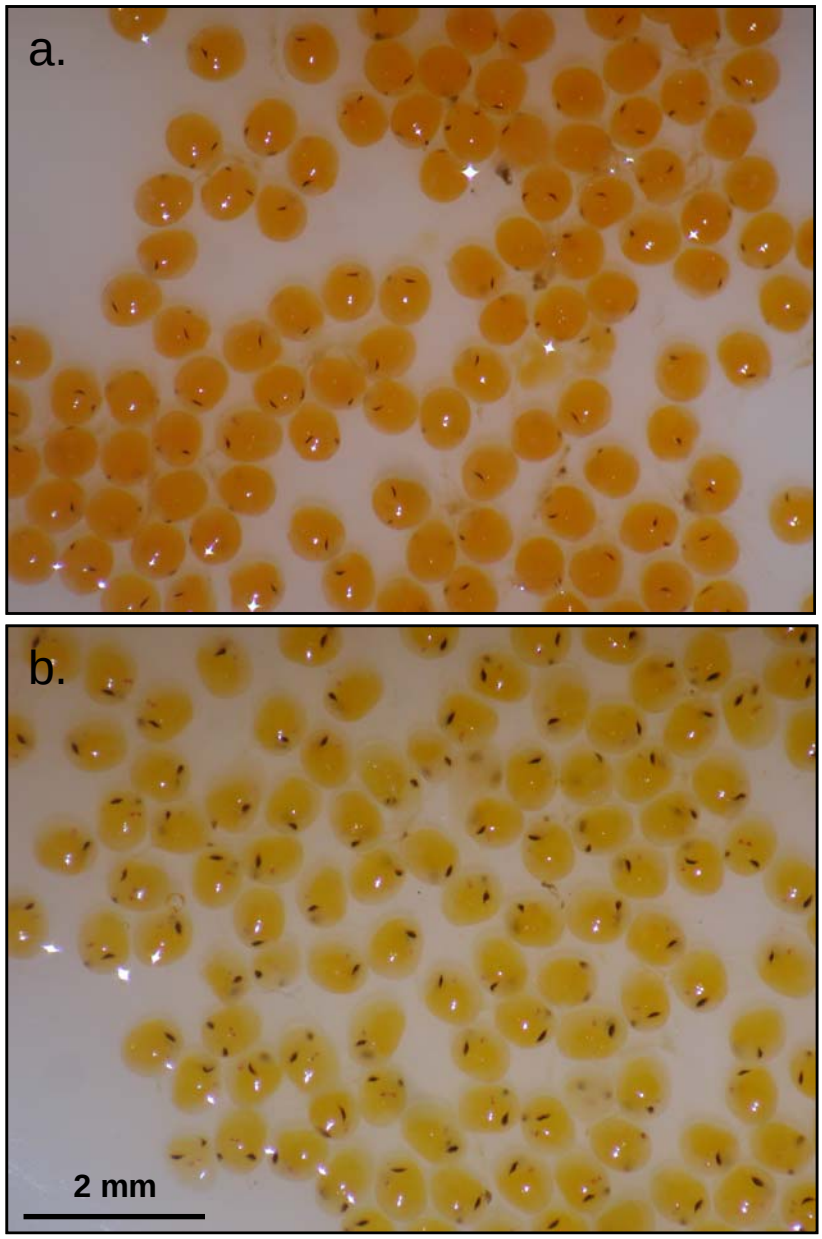


Plate 4.1. Photographs showing presence of eyespots on orange (a) and yellow (b) embryos of *T. australiensis* collected from south-eastern Australia.

Additional samples of reproductive females were collected in February 2003 to investigate aspects of reproductive output (i.e., fecundity, egg size, etc.,). To minimise egg loss both during and after sampling, all animals were kept alive in the field using buckets containing fresh seawater and then transferred into individual snap-lock plastic bags in the laboratory and frozen. To remove embryos from the female pleopods and dissolve the cementing material that binds eggs together, animals were immersed in a Petri dish containing a 1 - 2% household bleach solution (0.04 - 0.08% NaOCl) (after Choy, 1985). Following a period of less than 2 min, or when all the eggs were separated, the animal was removed from the Petri dish and the solution containing the eggs was poured over 100 μm mesh and rinsed with distilled water to neutralise the bleach. The egg mass, now containing separated eggs was removed from the mesh and placed onto the stage of a dissecting microscope and the eggs were counted. Following this, a sub-sample of approx n = 50 eggs was photographed with an Olympus Digital Camedia camera under 15x magnification. The images were then imported into the public domain image analysis program Image J v.1.29x (National Institutes of Health, USA) and calibrated using a digital photograph of a 0.1 mm increment stage micrometer at the same magnification (15x). When possible, the minimum and maximum diameter of approximately 50 eggs (n = 100) were measured for each ovigerous female using Image J.

4.2.2 Statistical analyses

Sex ratios of catches were compared between sites, sampling times and size classes, using chi-square (χ^2) tests. Female size at maturity for each population was determined as the smallest ovigerous female caught over the study period.

Analysis of variance (ANOVA) and Student-Newman-Keuls (SNK) tests were used to compare mean length of ovigerous females between sites. The relationships between latitude and size at maturity, mean size of ovigerous females, fecundity and embryo size were determined using least squares linear regression. Linear regressions were also used to investigate the relationship between; mean abundance and size at first maturity; mean abundance and mean size (CL) of ovigerous females; mean size (CL) of ovigerous females and number of embryos (uneyed, eyed and pooled); female size (CL) and egg size; and number of embryos and embryo size. All analyses involving embryos were done separately for both eyed and uneyed eggs, as well as for both egg types pooled. Differences in size between eyed and uneyed embryos were examined using separate *t*-tests for each site as unequal sample sizes between sites and egg types, meant a two-factor ANOVA was not appropriate. Analyses of covariance (ANCOVA) were used to compare; fecundity between ovigerous females carrying eyed and uneyed eggs and between populations; and, egg size between sites. All statistical analyses were performed using JMP (SAS, version 4) and NCSS 2000 (Jerry Hintze) statistical packages.

4.3 Results

4.3.1 Sex ratio

Sex ratios (male:female) of catches were influenced by site, time and size class. Overall, a prevalence of females across all sites, combined for all sampling times, resulted in sex ratios that were significantly ($P < 0.001$) skewed towards females at all sampling locations (Fig. 4.1). Comparisons through time for each site revealed that males never outnumbered females, with sex ratio biased towards females on all but one occasion (Old Man Island, October 2001, when sex ratio was approximately equal) (Table 4.2). This female bias was significant on many occasions for all sites, however patterns were not consistent between sites. For example, sex ratios were highly significant for most months between August and December 2001 and July and October 2002, at Maianbar, Cabbage Tree Basin and Shoalhaven Heads, but not at Old Man Island, Garlandtown and Quondolo Island (even though ratios were biased towards females at the latter site). A temporal pattern that was consistent across most sites was the reduction in abundance of females during May and June 2001, when sex ratios were significantly biased towards females at Maianbar only (Table 4.2).

When considering individual size classes (combined for all months), the smaller size classes (≤6 mm) were often significantly biased towards males across all sites, except for the Shoalhaven Heads site where only two individuals less than 6 mm were captured (Table 4.3). In the medium to large size classes, females were significantly more abundant than males across all sites, however, sex ratios started to become significant ($P < 0.01$) at smaller sizes at Garlandtown and Quondolo

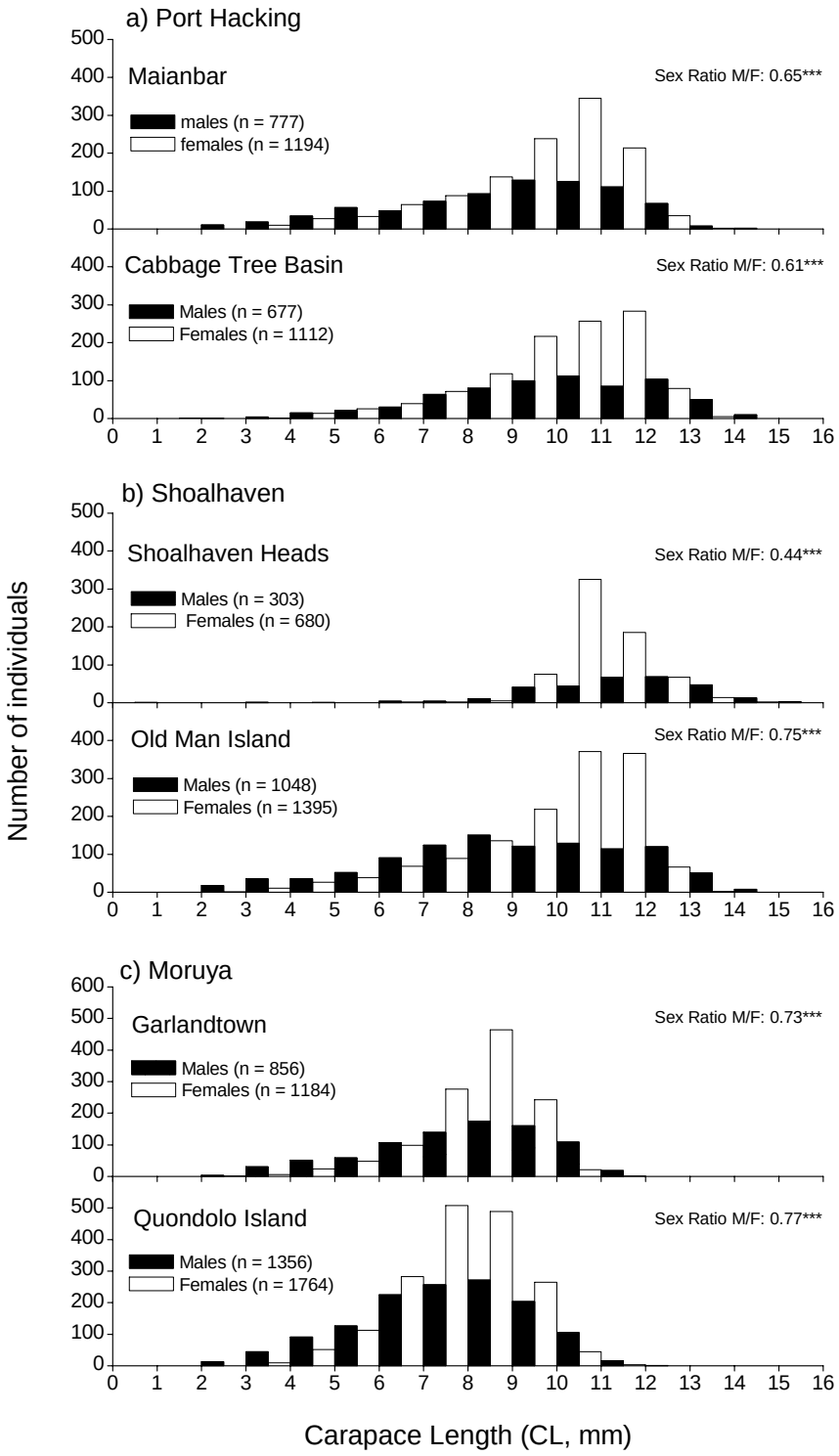


Figure 4.1. Size frequency distributions of male and female *T. australiensis* at sites within a) Port Hacking, b) Shoalhaven River and c) Moruya River pooled for all sampling occasions between January 2001 and January 2003. M/F sex ratio and significance level (χ^2: *** $P < 0.001$) shown.

Island, compared with sites in the Shoalhaven and Port Hacking (Table 4.3). For the largest size classes, an increase in male abundance resulted in sex ratios significantly biased towards males across all sites. However, the largest size class for the Garlandtown and Quondolo Island sites contained individuals that were smaller than individuals found at sites in either Port Hacking or Shoalhaven. This was the result of the smaller sizes of animals at these more southern locations (Fig. 4.1).

Table 4.2. Sex ratio of *T. australiensis* on each sampling occasion at Maianbar (MB), Cabbage Tree Basin (CTB), Shoalhaven Heads (SHH), Old Man Island (OMI), Garlandtown (GT) and Quondolo Island (QI) between January 2001 and January 2003. Asterisks indicate sex ratios significantly different from 1:1 (χ^2).

Month/Year	MB	CTB	SHH	OMI	GT	QI
Jan 01	0.57**	0.56*	0.44*	0.82	0.84	0.92
Feb	0.6*	0.44**	0.35**	0.57**	0.64*	0.64**
March	0.55**	0.75	0.53*	0.55**	0.60*	0.42***
May	0.65*	0.82	0.95	0.70	0.65	0.83
Jun	0.66**	0.72	0.61	0.73	0.69	0.91
July	0.75	0.57	0.43**	0.56***	0.63*	0.72*
Aug	0.51***	0.49***	0.33***	0.66**	0.87	0.53**
Sep	0.46***	0.54***	0.33***	0.95	0.83	0.76*
Oct	0.77	0.60**	0.41***	1.01	0.50***	0.93
Nov	0.64**	0.49***	0.59**	0.77	0.71*	0.90
Dec	0.74*	0.61**	0.29***	0.82	0.80	0.71**
Jan 02	0.85	0.71*	0.55**	0.73*	0.66**	0.79
Mar	0.46***					
Apr	0.66**					
Jun	0.49***					
Jul	0.60**	0.63*	0.44**	0.98	0.75	0.67**
Aug	0.53**					
Sep	0.93					
Oct	0.48***	0.59*	0.39***	0.76	0.82	0.88
Nov	0.79					
Dec	0.76					
Jan 03	0.83	0.70*	0.52**	0.67**	0.79	0.89

Table 4.3. Sex ratio of *T. australiensis* amongst different size classes at Maianbar (MB), Cabbage Tree Basin (CTB), Shoalhaven Heads (SHH), Old Man Island (OMI), Garlandtown (GT) and Quondolo Island (QI), combined for all sampling occasions between January 2001 and January 2003. Asterisks indicate sex ratios significantly different from 1:1 (χ^2).

Size Class	MB	CTB	SHH	OMI	GT	QI
1.1-2	0	0	0	0	0	0
2.1-3	0	0	0	18***	5	0
3.1-4	2	4	0	3.18*	5***	5.22***
4.1-5	1.21	1.07	0	1.4	2.30*	1.73**
5.1-6	1.73*	0.75	0	1.35	1.21	1.14
6.1-7	0.76	0.86	2	1.34	1.08	0.77**
7.1-8	0.79	0.87	2	1.42*	0.50**	0.52***
8.1-9	0.72*	0.68	2.2	1.08	0.38***	0.54***
9.1-10	0.52***	0.45***	0.56**	0.54***	0.66***	0.77**
10.1-11	0.38***	0.44***	0.13**	0.35***	5.25***	2.43***
11.1-12	0.52***	0.29***	1.11	0.32***	19***	5**
12.1-13	2.2*	1.51**	3.35**	1.92**	0	0
13.1-14	4	9.4**	6**	25***	0	0
14.1-15	0	0	0	0	0	0

4.3.2 Female size at maturity

The mean, median, minimum, and maximum sizes (CL) of ovigerous females for each site are shown in Table 4.4. All size parameters varied between locations and appeared to be related to latitude, with females caught at southern locations (Garlandtown and Quondolo Island) maturing at smaller sizes than those in the north (Shoalhaven and Port Hacking) (Table 4.4). For example, size at maturity (i.e., smallest ovigerous female) from the most southerly population (Quondolo Island) was 5.41 mm (CL), compared to 8.03 mm (CL) for the most northerly population (Port Hacking). Despite this apparent trend, size at maturity was not significantly related to latitude ($R^2 = 0.60$, $F = 6.09$, $P > 0.05$, n = 6), due to the larger size at maturity for the Shoalhaven Heads population. When data for the Shoalhaven Heads population is removed from the analysis, a significant negative correlation between latitude and size at maturity was evident ($R^2 = 0.86$, $F =$

18.5769, $P < 0.05$, n = 5), with size at maturity decreasing with increasing latitude (Fig. 4.2). This indicates that the Shoalhaven Heads population, which currently appears isolated and has low recruitment, may have quite different characteristics to the other *T. australiensis* populations studied.

For the mean size of ovigerous females, a general decrease in size from north to south was observed (Table 4.4). ANOVA revealed significant differences between sites ($P < 0.0001$), with SNK tests indicating that mean size at Shoalhaven Heads was significantly larger ($P < 0.05$) than at all other sites. Again, the larger size of ovigerous females at this site could be explained by the fact that small individuals were generally not captured (Fig. 4.1). Despite the anomaly at this one location, the mean size of ovigerous females was still significantly related to latitude (R^2 = 0.69, F = 8.8839, $P < 0.05$, n = 6), with mean size decreasing with increasing distance south (Figure 4.3).

There were no significant relationships between mean abundance and size at first maturity (R^2 = 0.64, F = 7.0709, $P > 0.05$, n = 6) or between mean abundance and mean size of ovigerous females (R^2 = 0.45, F = 3.3409, $P > 0.05$, n = 6).

Table 4.4. Size parameters of ovigerous females of *T. australiensis* for each site (Maianbar, Cabbage Tree Basin, Shoalhaven Heads, Old Man Island, Garlandtown and Quondolo Island) and averaged for each estuary (Port Hacking, Shoalhaven and Moruya), between January 2001 and February 2003. Standard errors shown in parentheses.

Site	Mean	Median	Minimum	Maximum	*N*
Maianbar	10.32 (0.08)	10.47	8.03	13.39	151
Cabbage Tree Basin	10.82 (0.08)	10.95	7.29	13.17	140
Shoalhaven Heads	11.12 (0.11)	11.06	8.34	14.9	87
Old Man Island	10.73 (0.09)	11	6.11	13.01	115
Garlandtown	8.54 (0.06)	8.59	5.77	10.69	245
Quondolo Island	8.27 (0.06)	8.23	5.41	11.1	273
Estuary					
Port Hacking	10.57 (0.06)	10.71	7.66	13.28	291
Shoalhaven	10.95 (0.07)	11.03	7.22	13.95	202
Moruya	8.40 (0.04)	8.41	5.59	10.89	518

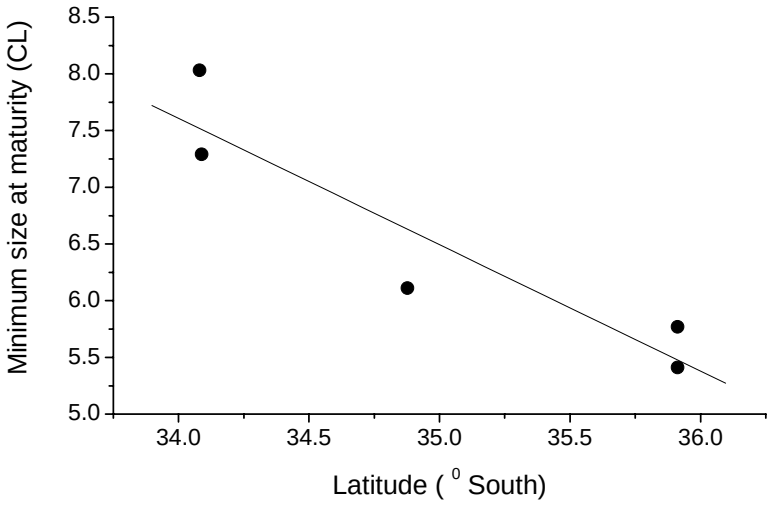


Figure 4.2. Relationship between female size at maturity (CL) of *T. australiensis* and latitude for each population (Shoalhaven Heads excluded), combined for all sampling occasions between January 2001 and February 2003.

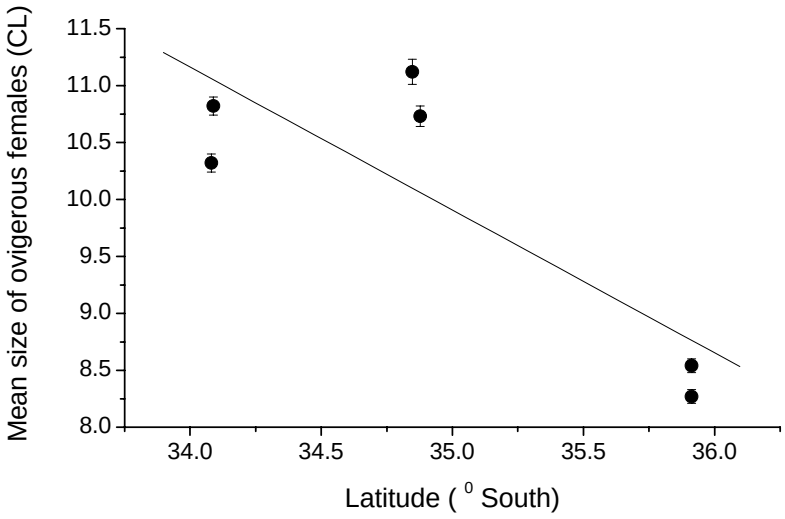


Figure 4.3. Relationship between mean size (CL) of ovigerous females of *T. australiensis* and latitude for each population, combined for all sampling occasions between January 2001 and February 2003.

4.3.3 Breeding season

Breeding season was determined by the proportion of ovigerous females in each population on each sampling occasion (Fig. 4.4). Reproductive period varied between estuaries and between sites within estuaries, with the main difference being between northern and southern populations. At Garlandtown and Quondolo Island (Moruya River), which were the southern most populations, breeding appeared to start earlier with ovigerous females carrying predominately uneyed eggs in January (mid-summer). Only small numbers of ovigerous females were present during January 2001 at sites in the Shoalhaven River, whereas almost no ovigerous females were present at sites in Port Hacking at this time. There were also a higher proportion of females carrying more developed eyed eggs during February 2001 at the southern sites compared to sites further north. In general, the percentage of ovigerous females peaked in January/February (mid-late summer) at

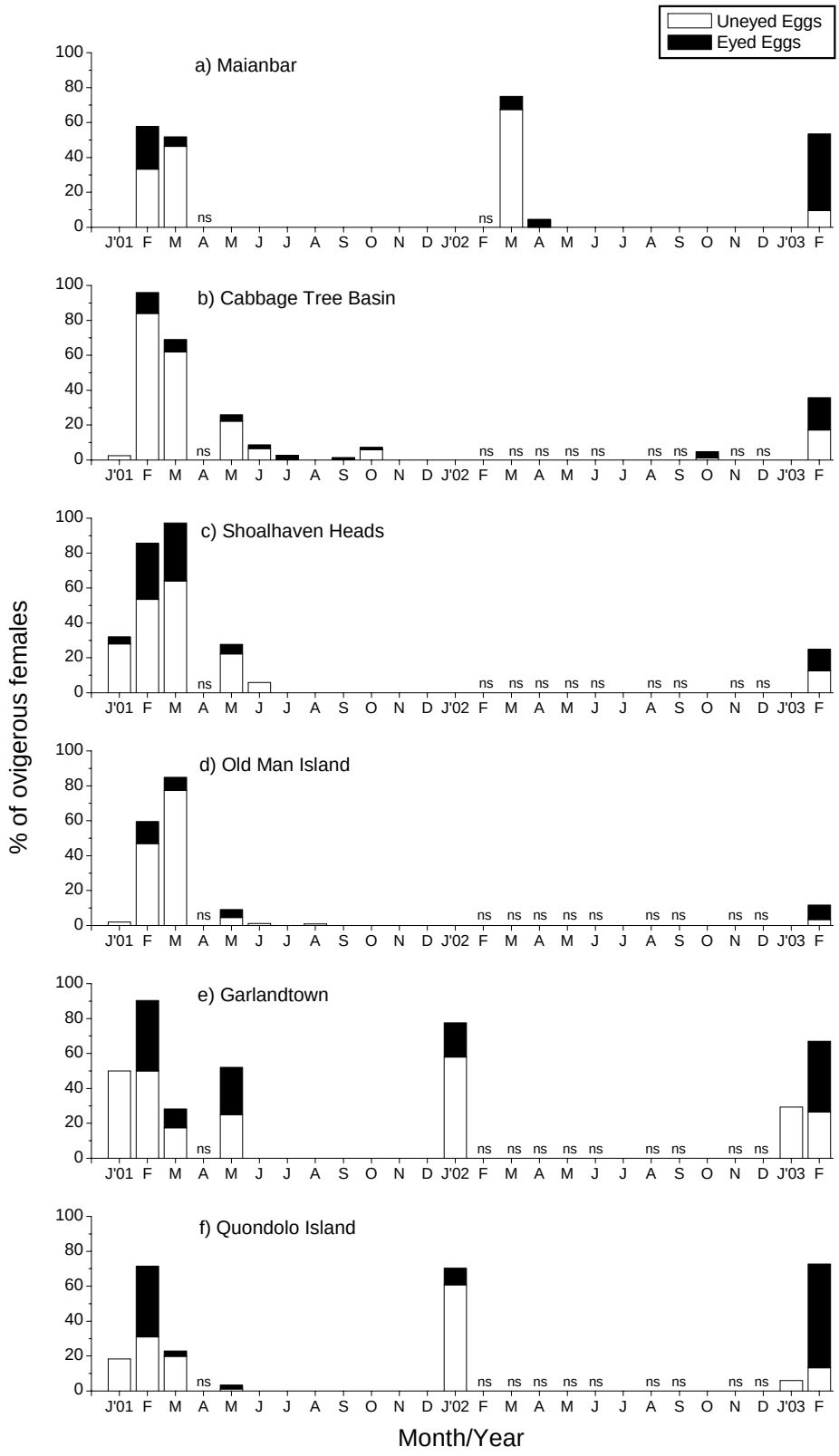


Figure 4.4. Percentages of ovigerous females of *T. australiensis* and proportion of eyed and uneyed embryos on each sampling occasion at a) Maianbar, b) Cabbage Tree Basin, c) Shoalhaven Heads, d) Old Man Island, e) Garlandtown and f) Quondolo Island between January 2001 and February 2003. ns = not sampled.

sites in the Moruya River and in February/March (late summer-early autumn) at sites in Shoalhaven River and Port Hacking.

The pattern of earlier breeding at southern locations was consistent between years. However, the percentage of ovigerous females varied between years for most sites, indicating differences in reproductive output between years (Fig. 4.4). For example, there were higher percentages of ovigerous females at the Moruya River sites during January 2002 than in January 2001, with samples in the second year also containing a higher proportion of eyed embryos. Similarly, more ovigerous females were present in samples from Maianbar in March 2002 compared to March 2001. However, in January and February 2003, there was a reduction in the peak of ovigerous females at most sites, particularly for the Shoalhaven River where less than 30% of females were ovigerous in February 2003, compared to 60 - 80% in February 2001. Furthermore, there were higher percentages of eyed eggs across all sites in February 2003, compared to the same month in 2001.

Breeding period also generally finished earlier at southern sites. No ovigerous females were present in samples in June at sites in the Moruya River (Fig. 4.4). Small numbers of females were ovigerous during June at sites in the Shoalhaven River. Breeding period was more continuous at the Cabbage Tree Basin site, with ovigerous females present through to July, but not August, with an apparent minor breeding period in September/October 2001 and October 2002. This pattern did not occur at Maianbar (the most northern site approximately 2 km from Cabbage Tree Basin), with breeding ending in April.

4.3.4 Effect of size on breeding season

Given that the sizes of reproductive females differed between sites (Table 4.4), the effect of size on breeding season was also investigated. Ovigerous females were grouped into 4 size classes; small (5.01 - 8 mm CL), medium (8.01 - 10 mm CL), large (10.01 - 12 mm CL) and extra large (12.01+ mm CL). At sites in Port Hacking and the Shoalhaven River there was always a higher percentage of large animals ovigerous at any particular time, with lower numbers of extra large, medium and almost no small ovigerous females (Fig. 4.5). In contrast, sites in the Moruya River always had a higher proportion of medium and small sized ovigerous females compared to large and extra-large individuals. Despite the obvious size differences in ovigerous females between sites, the results indicate that within each population, there was generally a higher proportion of larger sized females that were ovigerous at any particular time during the breeding season. Large and medium females also appeared to breed more continuously than small and extra-large animals across sites.

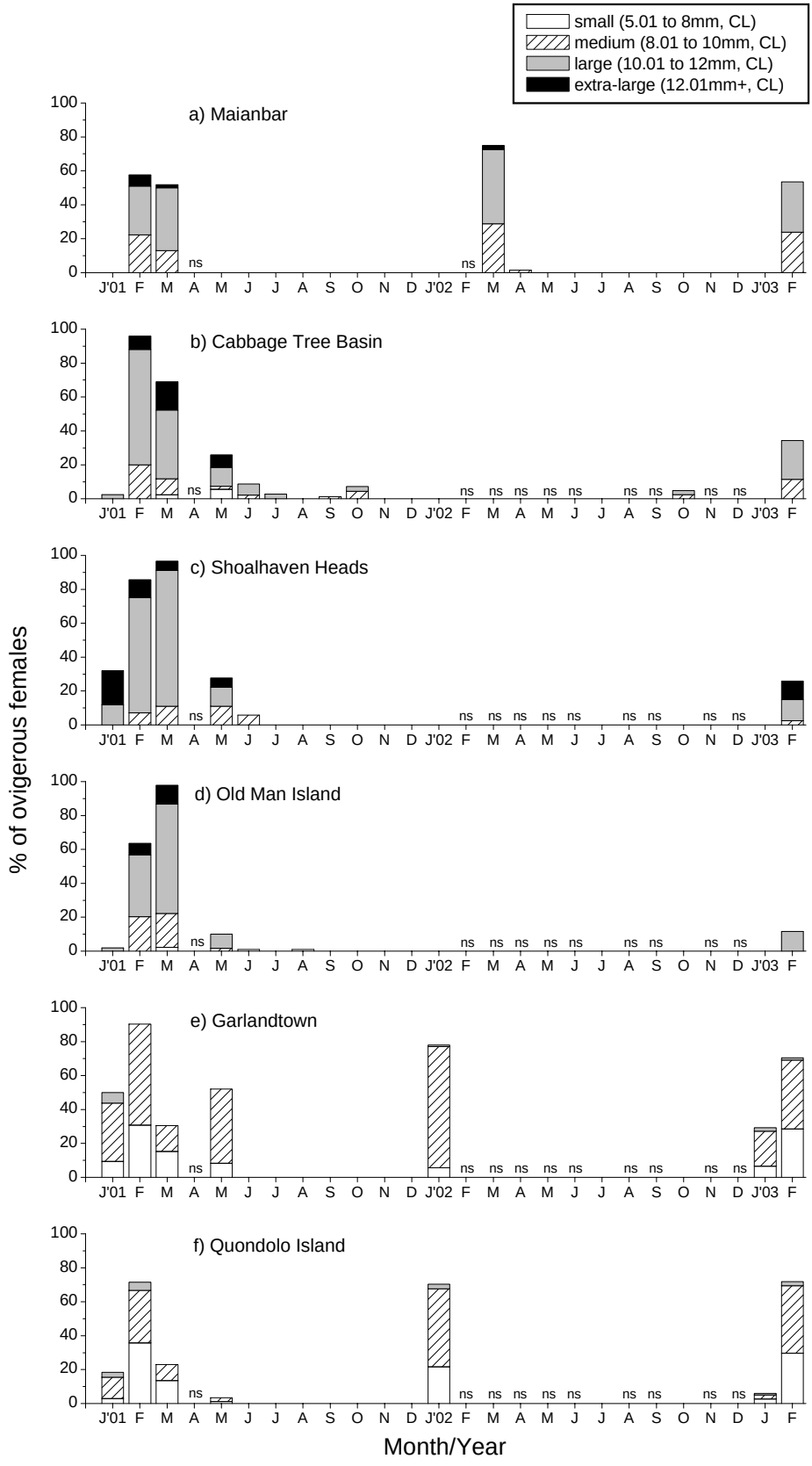


Figure 4.5. Percentages of ovigerous females of *T. australiensis* and proportion of small (5.01-8mm CL), medium (8.01-10 mm CL), large (10.01-12 mm CL) and extra-large (12.01+mm CL) individuals on each sampling occasion at a) Maianbar, b) Cabbage Tree Basin, c) Shoalhaven Heads, d) Old Man Island, e) Garlandtown and f) Quondolo Island between January 2001 and February 2003. ns = not sampled.

4.3.5 Gonad maturation

The macroscopic appearance of the ovaries of females throughout the study period was divided into 5 different categories based on the chronological sequence of development (see Materials and methods). For sites in Port Hacking and Shoalhaven River (Fig. 4.6), the percentage of stage 4 ovaries begins to increase during spring and summer and begins to decrease in late summer/early autumn (February/March) when ovigerous females appear in the populations. For sites in the Moruya River, the proportion of individuals with stage 4 ovaries was lower than for other estuaries. However, this may be related to the smaller size of individuals at these locations (Fig. 4.6). For example, a smaller body size may result in fewer oocytes in the ovaries and a less intense orange colour. Certainly, the proportion of mature females with stage 3 ovaries at Garlandtown and Quondolo Island followed a trend similar to that of females with stage 4 ovaries at sites in the Shoalhaven River and Port Hacking, in that the proportion of females with stage 3 eggs increased throughout the spring months before decreasing in summer when females become ovigerous (Fig. 4.6).

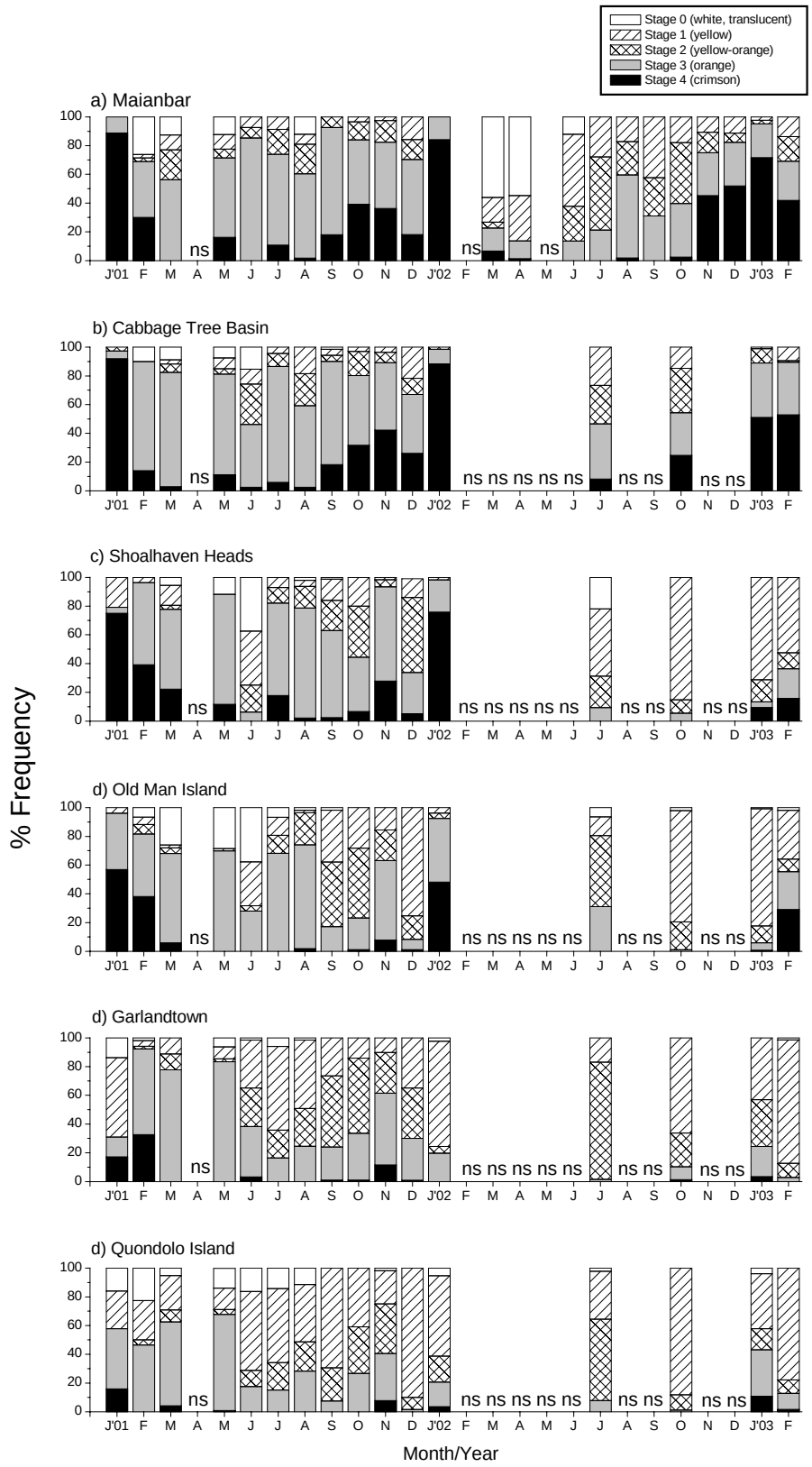


Figure 4.6. Percentages of mature females of *T. australiensis* with gonads at different stages of maturation on each sampling occasion at a) Maianbar, b) Cabbage Tree Basin, c) Shoalhaven Heads, d) Old Man Island, e) Garlandtown and f) Quondolo Island between January 2001 and February 2003. ns = not sampled.

4.3.6 Reproductive output

4.3.6.1 Fecundity

Fecundity was significantly higher for females carrying eyed embryos (x = 1638 ± 101) compared to females carrying uneyed embryos (x = 1182 ± 124) (ANCOVA; slopes: $F = 2.08$, $P > 0.1$; intercepts: $F = 4.29$, $P < 0.05$). Despite this, ovigerous females with both eyed and uneyed eggs were pooled to allow comparisons of fecundity between locations, since it was not possible to obtain approximately equal numbers of females of each egg stage from each site. The relationship between female size and fecundity increased linearly and was significant across all sites, with high correlations between carapace length and number of embryos (Fig. 4.7, Table 4.5). Given the small sample size (<10 individuals), no regressions were possible for the populations at Old Man Island in the Shoalhaven River, however the data appear to indicate a similar trend (Fig. 4.7d). The linear relationship between female size and number of eggs differed significantly between populations and the mean number of eggs per female was not significantly different between locations (ANCOVA; slopes: $F = 26.03$, $P < 0.0001$: intercepts: $F = 0.85$, $P > 0.1$). Even with the effect of carapace length on fecundity removed by ANCOVA, there was still a significant negative correlation ($R^2 = 0.93$, $F = 43.70$, $P < 0.01$, n = 5) between latitude and fecundity such that, as latitude increased fecundity decreased (Fig. 4.8).

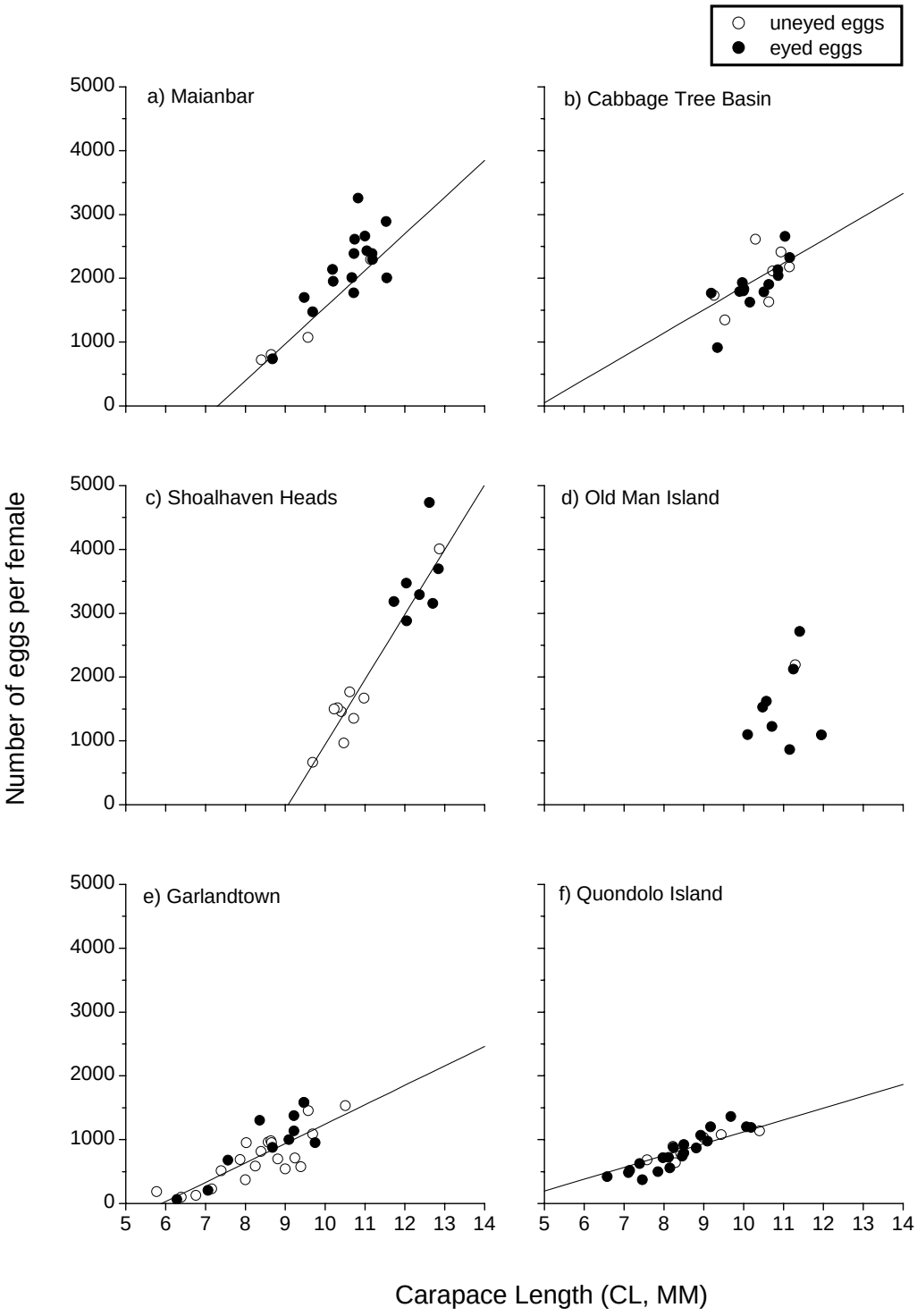


Figure 4.7. Relationship between number of embryos and carapace length (CL) of ovigerous females of *T. australiensis* at each site in February 2003 (See Table 4.5 for regression equations).

Table 4.5. Minimum, mean (±SE) and maximum number of embryos per female of *T. australiensis* and regression equations showing relationship between female size (CL) of and number of embryos (NE) for Maianbar, Cabbage Tree Basin, Shoalhaven Heads, Old Man Island, Garlandtown and Quondolo Island in February 2003. R^2, *F*-ratios and *P* values shown. N = number of shrimp.

Site	**No. eggs/female** min	mean (±SE)	max	**Regression equation**	R^2	*F*	*P*	**N**
Maianbar	723	1980.75 (160.56)	3259	NE = -4663.00 + 641.32CL	0.75	53.94	<0.0001	20
Cabbage Tree Basin	914	1926.95 (91.96)	2656	NE = -2679.70 + 446.88CL	0.48	16.93	<0.001	20
Shoalhaven Heads	663	2457.69 (307.01)	4738	NE = -9642.32 + 1059.95CL	0.89	110.17	<0.000	16
Old Man Island	863	1606.67 (206.21)	2714	-	-	-	-	9
Garlandtown	63	801.13 (81.49)	1091	NE = -1925.06 + 324.74CL	0.68	60.99	<0.001	31
Quondolo Island	371	828.85 (52.08)	1363	NE = -1319.49 + 253.56CL	0.82	113.77	<0.001	27

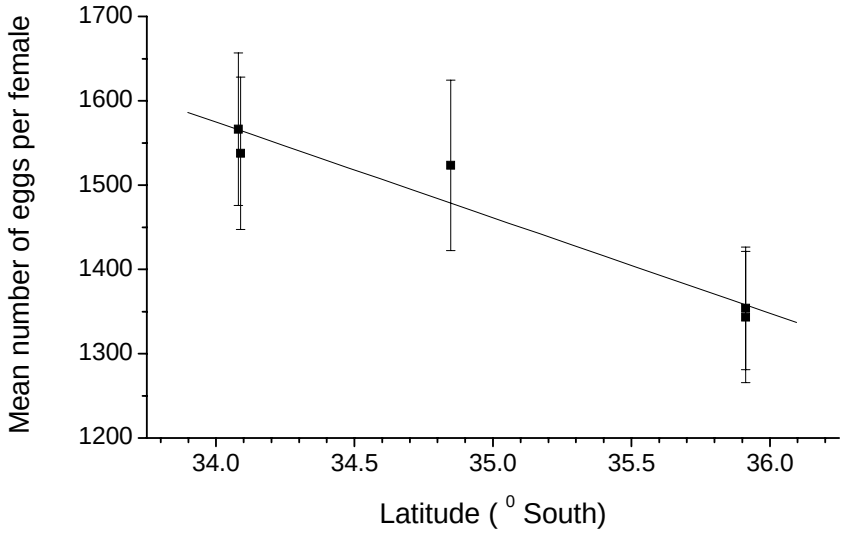


Figure 4.8. Relationship between the adjusted mean number of eggs per female of *T. australiensis* (effect of size removed by ANCOVA) and latitude for each population (Old Man Island excluded), for February 2003. Standard errors shown.

4.3.6.2 Egg size

There were significant differences between the size of eyed and uneyed embryos across all sites (Table 4.6). However, there were no consistent patterns in egg size between sites. At Maianbar and Cabbage Tree Basin, eyed eggs were significantly larger than uneyed eggs, whereas at sites in the Shoalhaven River (Shoalhaven Heads and Old Man Island), uneyed embryos were significantly larger. In the Moruya River, uneyed embryos were significantly larger than eyed embryos at Garlandtown, whilst at the Quondolo Island site, eyed embryos were significantly larger.

There was a significant positive linear correlation between the size of uneyed embryos and carapace length of females ($R^2 = 0.22$, $F = 9.5172$, $P < 0.01$, n = 36)

(Fig. 4.9). In contrast, there was no significant relationship between the size of eyed embryos and carapace length ($R^2 = 0.004$, $F = 0.2241$, $P > 0.05$, n = 52). For eyed and uneyed embryos combined, there was a significant relationship between egg size and carapace length, although predictably, the relationship was more variable than for uneyed embryos ($R^2 = 0.065$, $F = 6.1012$, $P < 0.05$, n = 88) (Fig. 4.9).

The diameters of uneyed embryos ranged from 0.642 mm at Maianbar to 0.566 mm at Quondolo Island and were highest at sites in the Shoalhaven River (0.670 mm and 0.654 mm respectively) (Table 4.6). Since egg size was correlated with carapace length for uneyed embryos (see above), the absence of smaller ovigerous females at Shoalhaven Heads may account for the larger mean egg size at this site. Smaller sized females were also captured at sites in Moruya (Fig. 4.1). ANCOVA was used to compare egg sizes between sites (removing the effect of female CL on embryo size) and found no significant differences in mean embryo diameter ($F = 1.92$, $P > 0.1$). Furthermore, least squares regression for adjusted means (ANCOVA) found no significant relationship between uneyed embryos and latitude ($R^2 = 0.34$, $F = 2.1442$, $P > 0.1$, n = 6).

The mean diameter of eyed embryos ranged from 0.635 mm at Maianbar to 0.618 mm at Quondolo Island and there were no significant differences in mean egg diameter between sites (ANCOVA, $F = 0.38$, $P > 0.1$) and no significant relationship between egg size and latitude ($R^2 = 0.121$, $F = 0.5497$, $P > 0.1$). Similarly, the diameter of eyed and uneyed eggs combined was not significantly different between sites (ANCOVA, $F = 1.77$, $P > 0.1$), and egg size was not

significantly related to latitude (R^2 = 0.43, F = 2.9991, P > 0.1). There was no relationship between the number of eggs and egg size for uneyed (R^2 = 0.097. n = 34, P > 0.05) and eyed (R^2 = 0.062, n = 50, P > 0.05) embryos (Fig. 4.10 a, b). However, for combined egg stages (i.e., eyed + uneyed eggs) there was a significant positive correlation, although the relationship was highly variable (R^2 = 0.074, n = 84, P < 0.05) (Fig. 4.10).

Table 4.6. Comparison of egg size between eyed and uneyed embryos of *T. australiensis* (*t*-test, *P* value shown) for each site (Maianbar, Cabbage Tree Basin, Shoalhaven Heads, Old Man Island, Garlandtown and Quondolo Island) in February 2003.

	Egg Diameter		
Site	**Uneyed**	**Eyed**	***P***
Maianbar	0.613 (*n* = 400)	0.644 (*n* = 1600)	<0.0001
Cabbage Tree Basin	0.614 (*n* = 700)	0.617 (*n* = 1300)	>0.1
Shoalhaven Heads	0.671 (*n* = 600)	0.635 (*n* = 700)	<0.0001
Old Man Island	0.654 (*n* = 100)	0.610 (*n* = 600)	<0.0001
Garlandtown	0.608 (*n* = 1300)	0.589 (*n* = 500)	<0.001
Quondolo Island	0.564 (*n* = 700)	0.628 (*n* = 700)	<0.001

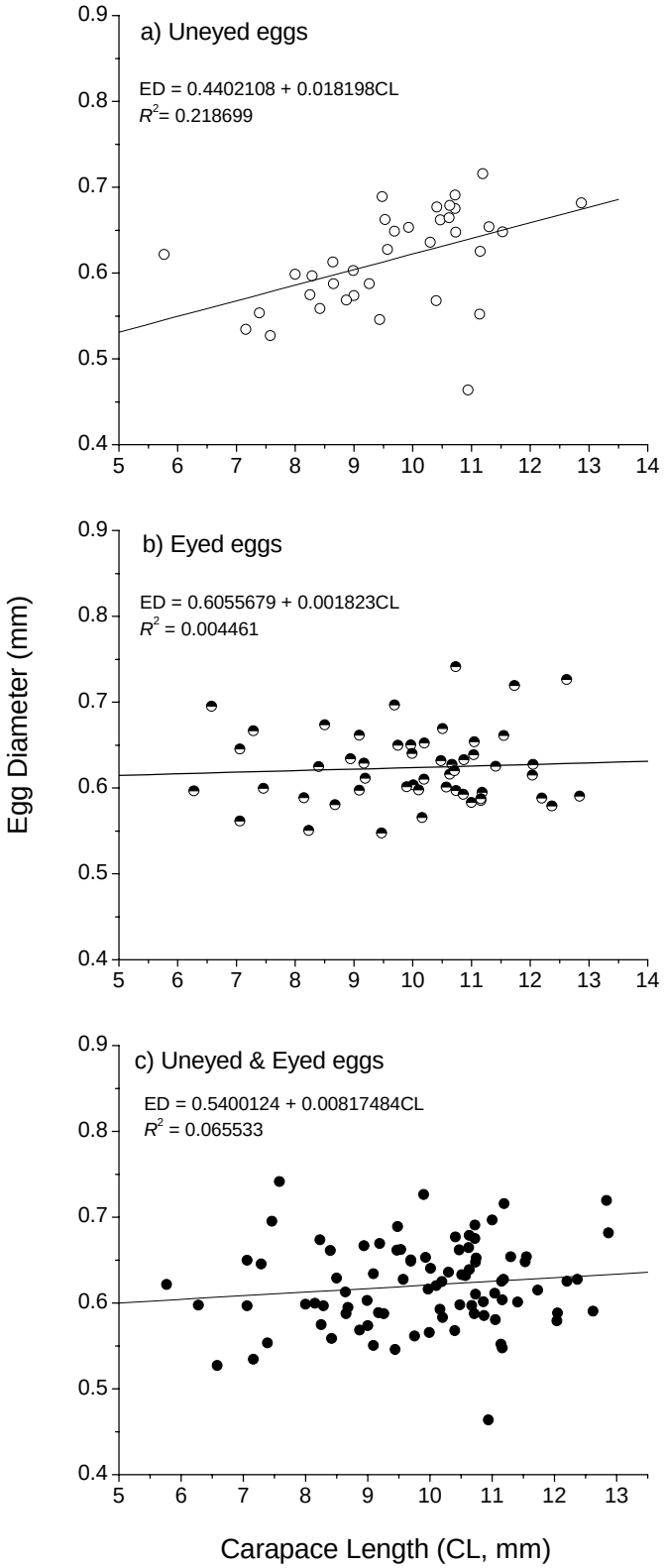


Figure 4.9. Relationship between egg size (diameter, mm) and carapace length (CL, mm) for a) uneyed, b) eyed and c) uneyed and eyed embryos of *T. australiensis*, pooled for all sites in February 2003. Regression equation and correlation coefficient (R^2) shown. ED = Egg diameter.

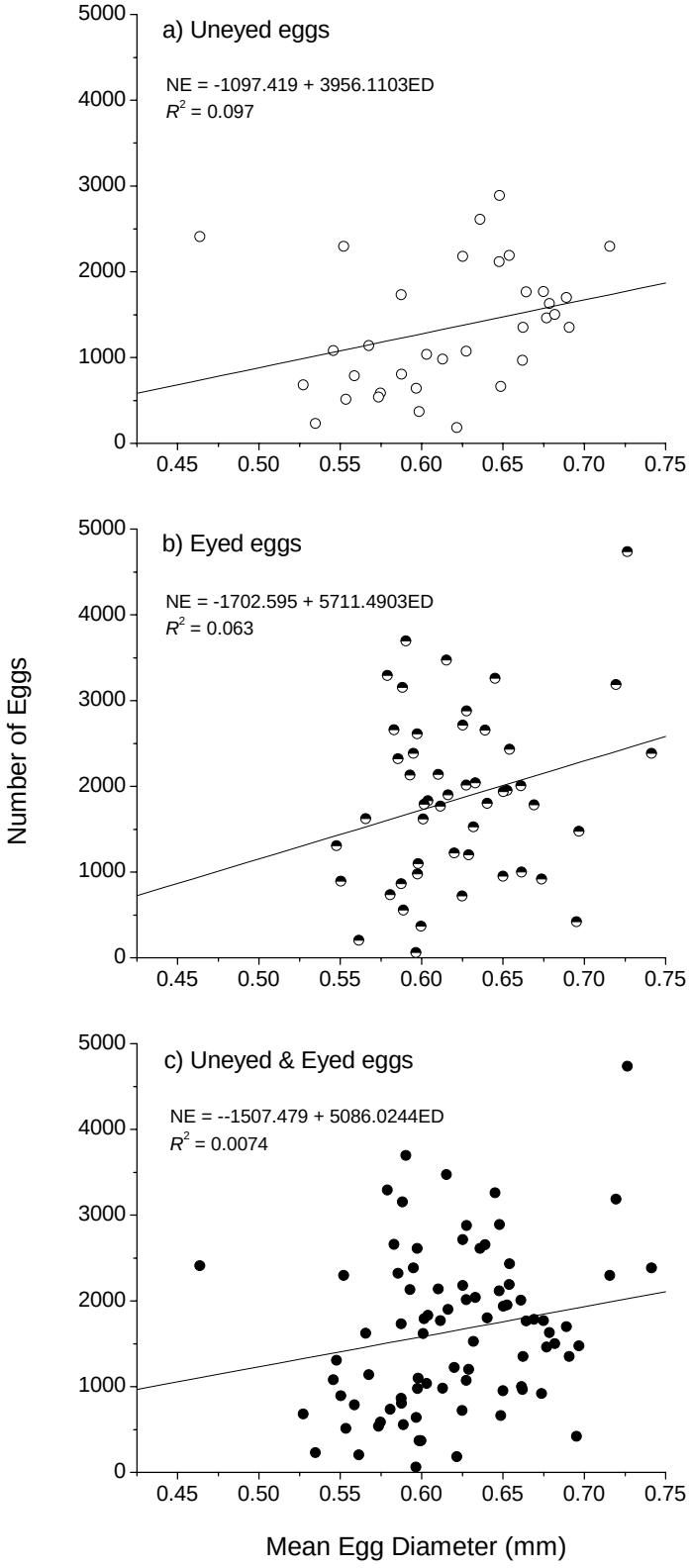


Figure 4.10. Relationship between number of eggs and egg size (diameter, mm) for a) uneyed, b) eyed and c) uneyed and eyed embryos of *T. australiensis*, pooled for all sites in February 2003. Regression equation and correlation coefficient (R^2) shown. NE = number of eggs, ED = egg diameter.

4.4 Discussion

The female-biased sex ratios in the present study are similar to findings from previous investigations of *T. australiensis* in Australia. Hailstone and Stephenson (1961) reported sex ratios as percentages of females in populations in Moreton Bay, which were between 51.5% and 66.5%. Similarly, Nurse (1980) found that a population in Port Hacking were 86% female, and Kenway (1981) reported male:female ratios of 0.38 – 0.77:1: for populations in Townsville. No previous single study of *T. australiensis* has documented temporal variations in sex ratio or spatial differences between size classes. In the present study, male:female sex ratios, combined for all months ranged between 0.44 - 0.77:1 across all locations. Sex ratios varied between months, with higher numbers of females during spring/summer periods across most sites (Table 4.2). Furthermore, there were consistent differences in sex ratio between size classes with male biased ratios for juvenile size classes (Table 4.3). However, at sexual maturity populations became significantly female-biased in all but the two largest size classes in each population. The largest two size classes were significantly biased towards males.

The finding of female-biased sex ratios following sexual maturity is common in previous studies of thalassinid population dynamics (Tunberg, 1986; Vaugelas *et al.*, 1986; Felder and Lovett, 1989; Hanekom and Baird, 1992; Dumbauld *et al.*, 1996; Tamaki *et al.*, 1997; Pezzuto, 1998; Souza *et al.*, 1998). Rowden and Jones (1994) suggested this might be related to the efficiency of sampling methods. However, Pezzuto (1998) highlighted that female-biased sex ratios have been reported across a range of different sampling methods, in both shallow and deep burrowing species, and for a range of different habitats. Furthermore, Rotherham

and West (2003) (see also Chapter 2 of this thesis) compared the length and weight of males and females of *T. australiensis* from different sampling gears and found that female-biased sex ratio most probably reflected the actual sex ratios and not method based selectivity. The general trend of female-biased sex ratio in the mature size classes of thalassinids has been related to a number of factors, such as the loss of males due to agonistic behaviour, predation of males leaving burrows in search of females and migration (Felder and Lovett, 1989; Dumbauld *et al.*, 1996). Agonistic behaviour has been noted for a number of thalassinid species (Hailstone, 1962; Tunberg, 1986; Rowden and Jones, 1994) and may result in selection of the best fighters and increase the probability of healthy males finding a female mate (Felder and Lovett, 1989; Pezzuto, 1998). Alternatively, Rodrigues (1983, cited in Pezzuto, 1998) suggested that fights may be due to the large investment in excavating and maintaining burrows. Nonetheless, the characteristics of agonistic behaviour and intra-specific combat of thalassinids are frequently limited to anecdotal accounts and hence the significance of such behaviour for mating systems is unknown.

Previous studies of *T. australiensis* have suggested that female-biased sex ratios may be related to local migrations of sexually mature females from other areas during breeding periods (Hailstone and Stephenson, 1961). However, no direct evidence of such movements exists, despite limited anecdotal accounts by local fisherman Hailstone and Stephenson, 1961and observations for other species (Monod, 1927). Such migrations of females from areas would result in both female and male-biased ratios in different sites. However, in the present study, female-biased sex ratios were common across a range of spatial and temporal

scales, indicating that migrations probably do not account for their biased sex ratio. Populations did become more significantly biased towards females during spring/summer months, which would have been expected if animals aggregated beneath the surface over small spatial scales within a sandflat, to mate during breeding periods (see Chapter 3). The role of migration in determining sex ratios in thalassinid shrimp warrants further research.

In this study, size at first maturity and mean CL of ovigerous females differed between sites and estuaries. Differences between estuaries were greater than between sites within estuaries, with southern populations maturing at smaller sizes than northern populations (Table 4.4). This result is surprising considering the well-documented relationship between increasing latitude (and decreasing temperatures) and increased body size and size at maturity for other marine invertebrate species (Kinne, 1970; Hastings, 1981; Jones and Simons, 1983; Levinton and Monahan, 1983). However, the present study was only conducted over approximately two degrees of latitude, within a temperate region. Mean temperatures between locations did not differ by more than 2°C. In addition, female size at maturity at Port Hacking and Shoalhaven River locations were similar to previous studies in Moreton Bay (Hailstone and Stephenson, 1961), which lies approximately 900 km north and within a sub-tropical climate zone. Consequently, the observed differences between northern and southern populations in the present study may not be a result of latitudinal or temperature differences alone.

Availability of food may influence female size at maturity, with higher competition at sites with low organic content or high population densities. Like many callianassids, *T. australiensis* is a deposit feeder and uses a sand sifting mechanism to extract detrital material, such as algae and diatoms from the sediment (Kenway, 1981). Berkenbusch and Rowden (2000) suggested that food availability was more important than environmental conditions in determining size at maturity for populations of *C. filholi*, with larger mean CL and size at maturity in populations where organic content was high. Similarly, Rowden and Jones (1994) found larger shrimp from organically enriched sites for populations of *C. subterranea*. Chittleborough (1976) suggested that high population densities inhibited growth in crayfish due to increased competition for food, and resulted in smaller sizes at maturity. Similarly, Kenway (1981) found that populations of *T. australiensis* from estuarine environments were more abundant and larger in size compared to sandy beach populations, where organic content was low. In the present study, both size at maturity and mean CL of ovigerous females appeared to decrease with increasing abundance (Figs. 4.2 and 4.3), however the relationships were not significant. Certainly, individuals in the Moruya River were not as large as individuals from northern populations (Fig. 4.1) and this site had some of the highest population densities in the study (see Chapter 3). Further research is required to determine the effect of population density, environmental factors and the availability of food on female size at maturity and to explain differences between northern and southern populations observed in the present study.

In this study, females were ovigerous throughout summer and autumn, with breeding commencing earlier in southern populations, compared to sites in estuaries furthest north (Fig. 4.4). Berkenbusch and Rowden (2000) found a similar pattern of earlier breeding at southern sites for populations of *C. filholi* in New Zealand, and attributed differences to food availability rather than temperature or other environmental factors. However, it is unlikely that food availability would account for such distinct and temporally consistent patterns for *T. australiensis*. For example, when data are combined for previous studies of *T. australiensis* in Australia, a latitudinal trend is apparent, with populations in the southern most range of the species' distribution, breeding earlier than populations at the northern most limits (Fig. 4.11). Some authors have argued that reproductive activity of some thalassinids does not occur during the hottest times of the year due to metabolic restrictions and anoxic conditions caused by high temperatures during low-tide periods (Tamaki *et al.*, 1997). However, summer breeding periods are common for many species of thalassinids (Table 4.1) and increases in temperature have been shown to initiate breeding periods of other marine invertebrates (Kinne, 1970). In the present study, breeding commenced during mid to late summer, but summer temperatures may not have been high enough in this region to negatively affect reproductive activity. In contrast, studies in Queensland found that *T. australiensis* commenced breeding during autumn (Fig. 4.11). Summer temperatures in sub-tropical regions of southern and central Queensland are higher than in temperate areas in south-eastern NSW and differences in timing between regions may be related to populations at lower latitudes delaying reproduction until autumn, when temperatures are cooler.

Alternatively, earlier breeding in southern regions may be related to the cooler climate causing longer incubation times, slower larval development and reduced growth rates (Wear, 1974). In fact, settlement and recruitment occurred

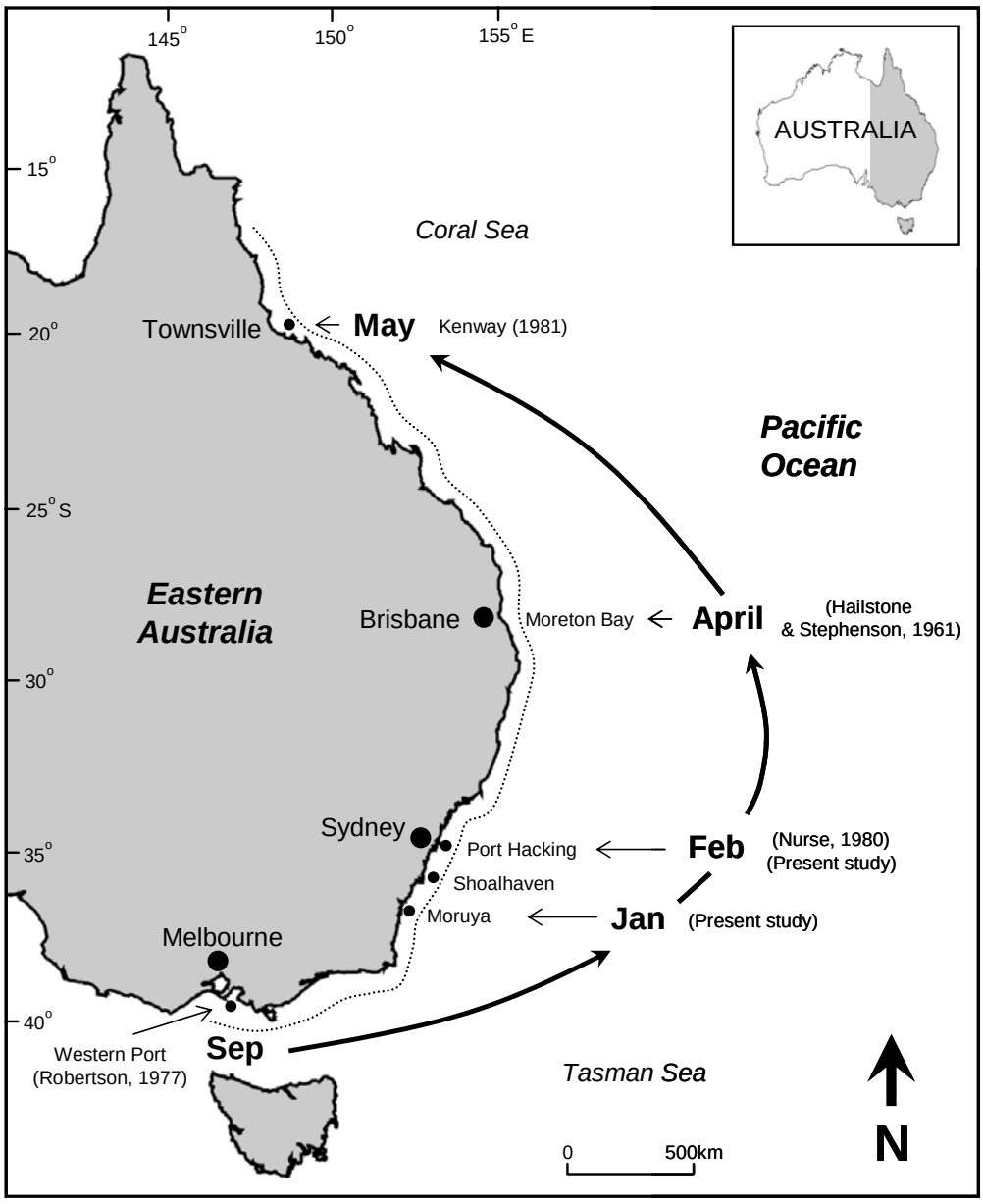


Figure 4.11. Latitudinal differences in the commencement of breeding seasons for *T. australiensis* in eastern Australia, based on data from the present study and previous research. Note the progressively earlier breeding from southern to northern locations. Dotted line shows species' distribution. Authors shown in brackets.

throughout spring and summer periods across all sites (see Chapters 3 and 5), suggesting that early breeding at higher latitudes may compensate for slower development (due to lower temperatures), thereby ensuring that settlement and recruitment occurs during spring/summer periods, when conditions are favourable. Equally, populations from higher latitudes may put more resources into reproduction due to lower growth rates and metabolic activity, resulting in earlier breeding periods (Kinne, 1970).

Despite the differences in initiation across a wide geographic range, breeding generally occurred throughout summer and autumn months (Fig. 4.4), which is common for many thalassinids (Table 4.1). This pattern was consistent between years, however reproductive effort was stronger in 2001 and 2002 across all sites. Recently, McPhee and Skilleter (2002a) found very small ovigerous females (~3 mm CL) all year round in Moreton Bay, which differs markedly to the results of the present and indeed all other previous studies. For example, Hailstone and Stephenson (1961) determined size at maturity to be 9 mm at the same locations sampled by McPhee and Skilleter (2002a), which is similar to the results in the present study (see Table 4.4). McPhee and Skilleter (2002a) hypothesised that very small ovigerous females were able to "*balance the metabolic demands of reproduction and respiration at higher temperatures than can larger females allowing them to reproduce in the warmer months*". However, the present study has shown that larger animals in south-eastern NSW are ovigerous during the peak of summer. It is quite likely that the ovigerous females caught by McPhee and Skilleter (2002a) were actually a closely related species, namely *Biffarius arenosa*, which reaches total lengths of around 40 mm and carapace lengths of

around 4 - 5 mm (see also Poore and Griffin, 1979; Poore, 1994). In the present study, *B. arenosa* was found in low numbers and females were ovigerous at similar sizes to the individuals reported by McPhee and Skilleter (2002a) (i.e., 3 - 5 mm) in Moreton Bay and also carried eggs at different times to *T. australiensis* (unpublished data). Further sampling or re-examination of previously collected individuals by McPhee and Skilleter (2002a) would resolve this disparity.

The duration of breeding seasons varied between and within estuaries (Fig. 4.4). In general, breeding period lasted 5 to 6 months with unimodal peaks in reproductive activity. Kenway (1981) and Robertson (1977) found similar results for populations in northern Queensland and Victoria respectively. However, previous studies have also reported bimodal peaks in reproductive activity for *T. australiensis*, resulting in extended breeding periods. For example, in Moreton Bay, Queensland, Hailstone and Stephenson (1961) found that *T. australiensis* had both a major and minor peak in reproductive activity, which extended the breeding period across nine months. Similarly, Nurse (1980) found bimodal peaks in breeding activity across a 10 - 11 month period for a population at Gray's Point in the upper reaches of Port Hacking. Despite a breeding season of around 5 - 6 months across most sites in the present study, an extended reproductive period occurred for the population at Cabbage Tree Basin (6 - 8 months), whilst reproductive activity for the population at Maianbar, just 2 km away, was considerably shorter (2 - 3 months). Taken together with previous studies, these results suggest that local population dynamics and interactions between physical environmental conditions within estuaries, may be important in determining the length of breeding seasons, and that differences at small spatial scales (i.e., within

estuaries) may be as great as differences across wider geographic ranges (i.e., between estuaries separated by hundreds of km).

For some thalassinids, female size has been shown to be an important factor in determining the commencement and duration of breeding seasons (Bird, 1982 cited in Dumbauld *et al.*, 1996), as well as the number of broods per season (Dumbauld *et al.*, 1996). In the present study, there were generally higher proportions of larger ovigerous females within populations, although size did not appear to affect the commencement of breeding seasons. Hailstone and Stephenson (1961) inferred from aquarium observations that females of *T. australiensis* carried eggs (i.e., incubation period) for a period of 6 weeks and suggested two periods of egg laying for populations in Moreton Bay, Queensland. A similar incubation period, was observed for specimens kept in aquaria at room temperature in the present study, with eggs that were initially orange-eyed (assumed to be less than 4 weeks old, see Fig. 4.4) hatching after a period of approximately 4 weeks. Attempts to get individuals to breed in aquaria proved unsuccessful, as there are difficulties in keeping animals alive for longer than 10 weeks.

Previous studies of other burrowing shrimp have inferred the number of consecutive broods per season per female, by dividing the incubation period (usually obtained from aquarium observations with constant temperatures and salinities) by the length of the breeding period (Hill, 1977; Dworschak, 1988). However, these calculations are only theoretical maximums and provide little insight into how many consecutive broods are actually carried by females. Results

from such calculations should be viewed with caution. For example, in field-based experiments involving captive individuals of *C. japonica*, Tamaki *et al.* (1996) found that females produced two broods per season. However, dividing the reproductive period (150 days) by incubation time (13-22 days) for this species (Tamaki *et al.*, 1997), yields 6.82 to 11.54 broods per season. The number of broods per season was not experimentally investigated for *T. australiensis* in the present study. However, the above calculations indicate theoretical maximums of between 3 and 5 broods per season, with this estimate varying between sites. In order to improve these estimates, further field based experimentation (after Tamaki *et al.*, 1996), is required for *T. australiensis*.

The present study demonstrated that fecundity was significantly higher for individuals carrying eyed embryos (Fig. 4.7), suggesting that females carrying uneyed embryos may not have finished depositing eggs. Previous studies of thalassinid fecundity often only count early stage eggs that do not have eyespots, as it is assumed that individuals with late stage embryos may be susceptible to egg loss. However, the results of the present study suggest that egg loss from females carrying late stage eggs is minimal and in fact, counting only uneyed embryos may lead to underestimates of fecundity (Fig. 4.7). Further work is required to compare fecundity between early and later stage embryos and attempt to sample equal numbers of females when comparing each egg type.

Despite the above differences, fecundity increased linearly with female size across all sites (Fig. 4.7). Relationships were more similar between sites within estuaries than between estuaries over a large geographic range (Table 4.5). These results

indicate that the largest individuals within populations are the most fecund and would not be protected by management strategies such as minimum size limits (Stewart and Kennelly, 1997). Although there were no significant differences in mean number of eggs per female between sites, there was a significant negative correlation between latitude and fecundity, which suggests that as latitude increased, fecundity decreased. A similar trend has been documented for other marine invertebrates and is often related to evolutionary theory, which predicts that comparably sized individuals produce more eggs in environments with elevated temperatures (Barnes and Barnes, 1965; Kinne, 1970; Lonsdale and Levinton, 1985; France, 1992; Gorny *et al.*, 1992; Lardies and Wehrtmann, 2001).

Estimates of between 63 and 4,738 eggs per female obtained for *T. australiensis* in the present study are similar to previous investigations in Australia. At a site in Port Hacking, several kilometres upstream from sites in the present study, Nurse (1980) found that a small number (n = 10) of mostly large individuals of *T. australiensis* carried between 4,134 and 8,126 eggs per female. In the northern most limit of the species' distribution, Kenway (1981) reported that ovigerous females carried between 93 and 2,236 eggs per individual. These existing studies do not suggest increased fecundity of *T. australiensis* in areas characterised by higher temperatures. However, they do indicate that differences in fecundity at smaller spatial scales, such as within estuaries, may be as great as variations across larger spatial scales, such as between estuaries.

Embryo size differed between eyed and uneyed eggs but these differences were not consistent between sites (Table 4.6). This result is surprising considering egg

sizes of crustaceans generally increase during incubation and development (Kinne, 1970; Wear, 1974). An explanation for the significantly larger size of uneyed embryos at some locations may be attributed to the bleach solution used to separate eggs, which may have caused early-stage embryos to swell. There were no significant differences in egg sizes between the various locations. Previous studies have also shown that differences between egg sizes are not expected for crustacean eggs from temperate climates (Wear, 1974). Sizes of uneyed embryos were smaller at sites within the Moruya River, which is not consistent with studies that have shown that incubation time increases as latitude increases (and temperature decreases), resulting in larger egg sizes (Efford, 1969; Wear, 1974; Berkenbusch and Rowden, 2000; Lardies and Wehrtmann, 2001). This might be explained by a number of other factors. For example, the higher population densities at sites in the Moruya River may have resulted in increased competition for resources and selection for smaller egg sizes. Secondly, it may also be related to the smaller size of individuals at these sites, as egg size was correlated with carapace length for uneyed embryos. Finally, embryo size was also correlated with number of eggs for combined egg stages (i.e., eyed + uneyed eggs), suggesting that the smaller size of embryos at the Moruya River sites may also be explained by the lower fecundity, which was directly related to the smaller size of individuals within this estuary.

The results of this study indicate that *T. australiensis* employs a strategy of relatively high fecundity and small egg size compared to other burrowing shrimp (see Table 4.1). Large numbers of eggs and small egg sizes are often associated with extended planktonic larval development for thalassinids (Table 4.1). Larval

development was not documented in the present study, as larvae did not survive longer than 24 hours after hatching in aquaria. However, previous studies have suggested that *T. australiensis* has one of the longest development times of the Thalassinidea. In fact, such a dispersal strategy may explain the widespread distribution of *T. australiensis* in eastern Australia (Kenway, 1981). Certainly, the patterns of post-larval settlers and recruits following the occurrence of ovigerous females in the present study indicate a long larval life (see Chapters 3 and 5). Future studies should attempt to determine larval development times in the laboratory, over a range of different temperatures and salinities.

The present research found considerable intra-specific variation in the reproductive biology of *T. australiensis* across a range of spatial and temporal scales in south-eastern NSW. Specifically, populations between widely separated estuaries showed differences in female size at maturity and commencement of breeding seasons. Despite this, breeding occurred throughout summer/autumn periods across populations, and the duration of breeding seasons varied both between and within estuaries. These patterns were generally consistent between years. Other aspects of reproduction, including female-biased sex ratios for mature size classes were also consistent across populations. Fecundity was related to female size and these relationships differed between populations, although number of eggs per female was not significantly different between locations.

The results of the present study would be of particular interest to fisheries managers in the implementation of management strategies involving size restrictions and/or temporal closures, but they also raise some interesting

questions for researchers. For example, temperature differences may explain the variability in size at maturity and the commencement and duration of breeding cycles. However, availability of food through either increased competition due to high population densities, or habitat quality may also affect these and other parameters including fecundity and egg size. Specific directions for further research on the reproductive biology of *T. australiensis* are summarised in Chapter 7. This chapter also includes discussions relating to the life-history and management of *T. australiensis* in NSW.

Chapter 5

Relative growth and preliminary estimates of absolute growth parameters, mortalities and exploitation ratios of *Trypaea australiensis* in south-eastern Australia.

5.1 Introduction

Estimating growth rates and age is a principal component of stock assessment procedures and management of harvested populations of marine organisms (Hilborn and Walters, 1992; King, 1995; Jennings *et al.*, 2001). Examination of striations or "growth rings" contained within hard structures of finfish, such as otoliths, scales, vertebrae and opercula, frequently allow accurate determination of age and growth (Nammalwar, 1974; Nordeng and Jonsson, 1978; Fossum *et al.*, 2000; Campana, 2001). Similarly, many invertebrates also possess permanent hard structures that record growth (Hartnoll, 1982, 2001), including the statoliths of squids (Jackson *et al.*, 2000), jaws of polychaetes (Britaev and Belov, 1993), shells of bivalve molluscs (Ropes and O'Brien, 1979) and genital plates of sea urchins (Gebauer and Moreno, 1995). Decapod crustaceans lack any permanent structures on which growth is recorded, as the old exoskeleton is shed and replaced by a new one during moulting, making determination of age difficult. Consequently, the discontinuous growth of decapod crustaceans is often described in terms of the increase in size occurring at a specific moult (moult increment) and the frequency of moulting (intermoult period) (Aiken, 1980; Hartnoll, 1982, 2001).

Despite the inherent difficulty, a number of techniques exist for determining age and growth of decapod Crustacea (reviewed by Hartnoll, 1982, 2001). Moult increment and intermoult period can be measured from captive individuals. However, the variability of these parameters in response to extrinsic factors may limit the applicability to wild populations, unless experiments measuring responses to specific stimuli are conducted under controlled conditions. Tag/recapture data provides information on growth of large decapods at liberty with respect to time, but provides no information on the time between tagging and moulting (Stewart and Kennelly, 2000). In these circumstances, moult frequency is often derived from approximations using a number of different methods (see references in Stewart and Kennelly, 2000). For some crustaceans, particularly small non-economic or cryptic species, the applicability of tagging programs may be limited, given the unsuitability of traditional tagging methods, as well as the absence of commercial or recreational fisheries to provide adequate returns (Hartnoll, 1982; Grant *et al.*, 1987). Studies on captive individuals of some crustaceans may also be problematic, particularly for species that are difficult to maintain in aquaria, or when such facilities are unavailable or expensive to set up.

Size frequency analysis may be used to estimate growth parameters for crustaceans that cannot be easily aged using captive experiments or tagging programs. This method relies on identifying modes in length frequency distributions, which are assumed to represent recruitment cohorts and age classes (Hartnoll, 2001). A single “snapshot” sample may be taken to determine the number of year classes in a population, or preferably, a series of data sets obtained at several different times to follow modal progression. If recruitment occurs in

discrete, annual pulses, identification of non overlapping year classes is relatively simple (Grant *et al.*, 1987; Hartnoll, 2001). However, for many species, reproduction and recruitment may occur over extended time periods, resulting in overlapping year classes, which makes assignment of age classes difficult (Grant *et al.*, 1987).

A number of computer programs including ELEFAN (Pauly and David, 1981), MULTIFAN (Fournier *et al.*, 1990) and MIX (Macdonald and Pitcher, 1979; Macdonald and Green, 1988) have been developed to estimate growth parameters, based on the best-fit of length frequency data. ELEFAN is a widely used package in these types of analyses. Nevertheless, there are questions relating to the reliability of this approach, given assumptions imposed on analyses and the subjectivity involved in interpreting results for difficult data (Hampton and Majkowski, 1987; Castro and Erzini, 1988; Isaac, 1990, Hartnoll, 2001). In fact, some authors argue against using length-frequency analysis in the absence of age-length keys derived from the age structure of catches (Castro and Erzini, 1988). However, some estimates of growth parameters are often still desirable, particularly for invertebrates that cannot be aged from hard parts or tagging studies. In this situation, it has been recommended that data sets show at least some evidence of progressing modes (assessed essentially by eye), together with some biological information, before proceeding with analyses (Castro and Erzini, 1988).

Growth of crustaceans has traditionally been modelled using the von Bertalanffy growth function (VBGF), despite its assumption of continuous growth, which

produces smooth growth curves. Some authors question the appropriateness of the VBGF for describing the discontinuous nature of crustacean growth (Breen, 1994; Mytilineou *et al.*, 1998). Others present a convincing argument for the continued use of VBGF for modelling the growth of crustaceans, pointing to the fact that estimates of the growth coefficient (k) and asymptotic length (L_{∞}) provide useful inter-specific comparisons (Stewart and Kennelly, 2000). Alternative models that consider the step-wise growth of crustaceans have also been investigated by several authors (McCaughran and Powell, 1977; Annala and Bycroft, 1980; Chen and Kennelly, 1999; Stewart and Kennelly, 2000). These step-wise approaches however, utilise data on moult increment and moult frequency, derived from studies of captive individuals and tag/recapture data.

Few studies have considered absolute growth parameters of burrowing thalassinid shrimp. Seemingly, no study has attempted to derive estimates of moult increment or moult frequency using both traditional external tagging methods and captive experiments, commonly employed on large decapods (Chen and Kennelly, 1999; Stewart and Kennelly, 2000). Dworschak (1988) determined moult frequency and increment for *Upogebia pusilla* in aquaria, based on the presence and measurements of successive discarded exuviae. The difficulty in determining moult increment and frequency is most likely the result of: i) the burrowing existence of thalassinids, which makes external tagging methods difficult; ii) the small size and fragility compared to large commercially important species; and, iii) the difficulty in maintaining captive individuals in aquaria (see Appendix 1).

Despite the difficulties in applying traditional tagging methods and captivity studies, von Bertalanffy growth curves based on electronic analyses of length frequency data have been constructed for only a few thalassinids, of which most use the ELEFAN package (see Dworschak, 1988; Pezzuto, 1998; Souza *et al.*, 1998). Dumbauld *et al.* (1996) carried out cohort analysis using the MIX software package, but did not provide von Bertalanffy growth curves. A number of other studies on burrowing shrimp have conducted graphical cohort analyses, essentially by eye, using length frequency distributions to derive estimates of life-span (Hailstone and Stephenson, 1961; Devine, 1966; Forbes, 1977a; Felder and Lovett, 1989; Rowden and Jones, 1994; Berkenbusch and Rowden, 1998; Kinoshita *et al.*, 2003). This method may underestimate longevity due to crowding of cohorts over larger size ranges. The problem of obtaining large and representative samples of shrimp (see Chapter 2), has perhaps restricted wider application of electronic length frequency analysis. Like previous studies on other populations parameters of thalassinid shrimp, such as relative abundance and reproductive biology (see Chapters 3 and 4), existing studies of growth have often been conducted on restricted spatial scales, such as single sites and estuaries. Clearly, there is much scope for estimating growth parameters of thalassinids using electronic length frequency analyses over a wider range of spatial and temporal scales, in order to investigate latitudinal and/or geographical differences that may exist within a species' range.

The change in shape of crustaceans with increasing growth is known as relative or allometric growth (Hartnoll, 1982). Paradoxically, the stepwise growth of crustaceans makes them particularly amenable to studies of relative growth

compared to investigations of absolute growth rates and age (see above). It is not surprising that many biometrical and morphometric studies involve decapod crustaceans (Hartnoll, 1982). Different patterns of relative growth of the decapods can result in sexual dimorphism (Minagawa, 1993; Mantelatto and Fransozo, 1994; Grandjean *et al.*, 1997; Mantelatto and Martinelli, 2001), heterochely (Abbey-Kalio and Warner, 1989; Labadie and Palmer, 1996; Pynn, 1998; Tsuchida and Fujikura, 2000) and may indicate the onset of sexual maturity and critical moults (Hartnoll, 1974, 1982; Weber, 1994; Sampredo *et al.*, 1999; Negreiros-Fransozo *et al.*, 2003). For example, prior to the puberty moult in decapods, growth of the primary chela in males and female is generally similar, being isometric or allometric (Hartnoll, 1974, 1982). Following sexual maturity, growth of the male chela becomes increasingly allometric, resulting in an increase in relative size. In females, growth remains isometric or negatively allometric, resulting in a sexually dimorphic and heterochelous chela, which may differ in form and function (see review by Mariappan *et al.*, 2000).

Although few studies have considered absolute growth parameters for burrowing thalassinid shrimp (see above), previous investigations have often focused on various aspects of relative growth. In particular, the most common analyses have involved determining size at maturity from relationships between carapace length and chela width or height (Hailstone and Stephenson, 1961; Devine, 1966; Dworschak, 1988; Felder and Lovett, 1989; Rowden and Jones, 1994; Dumbauld *et al.*, 1996; Berkenbusch and Rowden, 1998; Dworschak, 1998; Pinn, 2001). Regressions are computed for each sex and subdivided at transition points calculated using various methods (e.g., Pezzuto, 1993), which indicate changes in

relative growth and sexual maturity. Like other decapods (see above), relative growth of the major chela of burrowing thalassinid shrimp is often similar up to a transition point, before becoming positively allometric for males and negatively allometric or isometric for females, resulting in marked sexual dimorphism (Felder and Lovett, 1989; Lovett and Felder, 1989).

Data on relative and absolute growth parameters are lacking for *T. australiensis* in Australia, particularly for south-eastern NSW. The growth rates and longevity of *T. australiensis* in Moreton Bay, Queensland, have been estimated primarily from graphical analyses of length frequency histograms (Hailstone and Stephenson, 1961). This is really a preliminary approach (see above), and problems can occur, particularly where overlapping of successive cohorts are found. Preliminary investigations of internal tagging methods for *T. australiensis* appear promising for future studies seeking to determine moult increment and frequency (see Appendix 1) However, further research is required to maintain individuals in aquaria for extended periods and carry out large-scale tagging, which was beyond the scope of this study. At present, determining growth parameters for *T. australiensis* is largely reliant on electronic analyses of length frequency data.

While aspects of relative growth have been investigated for *T. australiensis* in Moreton Bay (Hailstone and Stephenson, 1961), parameters are likely to differ in southern regions. This may have important implications concerning implementation of traditional management strategies such as minimum size limits. Previous chapters of this thesis have provided new information on aspects of the population biology and ecology of *T. australiensis*, including abundance and

reproduction, from a spatially and temporally replicated sampling program in south-eastern Australia. The final component of this sampling program includes measurements and analyses of relative and absolute growth parameters, mortalities and exploitation ratios derived from quantitative biometric and length frequency data, which are considered in the present chapter.

5.2 Materials and methods

5.2.1 Measurements

Measurements of growth were taken from samples of *T. australiensis* collected in the main sampling program (see Chapter 3) using digital vernier callipers (0.01 mm) and included:

- Carapace length (CL, in mm): measured from the tip of the rostrum to the end of the carapace.
- Total length (TL, in mm): measured from the tip of the rostrum to the posterior margin of the telson.
- Chela height (ChH): of the propodus of the major chela at the widest point from the ventral to the dorsal margin.
- Chela width (ChW): of the propodus of the major chela along the midline from carpus to the insertion of the dactylus.

Additional measurements included;

- Wet weight (WW): measured to 0.01g .
- The side (left/right) of the major chela was also recorded.

Hailstone and Stephenson (1961) investigated the presence of recently moulted or "soft" individuals in field samples from Moreton Bay. Although the present study also intended to identify recently moulted individuals, it became clear that doing so was a highly subjective process. In fact, after defrosting field samples stored in the laboratory it could be argued that all samples were in fact "soft". Given the degree of subjectivity involved, estimates of moult frequency were not determined from field samples.

5.2.2 Statistical analyses

The computer program REGRANS (Pezzuto, 1993) was used to perform regression analyses on relative growth. This program contains most of the statistical techniques common to bivariate studies of relative growth, in a single package. However, analyses are limited to 1000 data pairs, which were randomly selected. Prior to analyses, data were checked for normality using Kolmogorov-Smirnov tests. After satisfying the assumptions of a normal distribution, standard least squares regressions were carried out on untransformed data (Lovett and Felder, 1989). Following this procedure, REGRANS was used in an iterative process to determine the transition point, which splits data in two segments corresponding to changes in relative growth. Acceptance of transition points follows further statistical tests contained within the package including:

- a test to ensure the slope of each line to the left and right of the transition point is significantly different from zero.
- a test to determine whether the sum of the squared residuals on Y of the lines to the left and right of the transition point is significantly smaller than the sum of the squared residuals for the whole data set.

- Analysis of covariance (ANCOVA) to test if the two segments are significantly different, confirming presence of a transition point.

Least squared regressions of log-transformed subdivided data were then performed to obtain allometric coefficients (Lovett and Felder, 1989) and determine type of relative growth (i.e., negatively allometric (<1), isometric (=1) or positively allometric (>1) (Huxley, 1932). Selected comparisons between slope and intercepts of regression lines including male v female and upper v lower regression lines were conducted using ANCOVA.

Parameters of the von Bertalanffy growth model were estimated for each site (combined for males and females) by performing the ELEFAN I routine of the FiSAT II package (Gayanilo *et al.*, 1995), on temporal length frequency data. This model has the basic form:

$$L_t = L_\infty[1\text{-}\exp(1\text{-}k(t\text{-}t_0))]$$

where L_t is the length (carapace length, mm) at time t; L_∞ is the asymptotic length (length at time infinity) and k is the growth coefficient. The theoretical age at length zero (t_0) is not estimated by ELEFAN I and was therefore computed using the equation of Lopez Veiga (1979, cited in Pezzuto, 1998):

$$t_0 = (1\text{-K})\ \ln\ (CL_\infty\text{-}CL_h/\ CL_\infty)$$

where CL_h is carapace length at hatching. Pezzuto (1988) suggested that larval carapace growth of a closely related callianassid, *Sergio mirim*, does not fit the

VBGF growth function, and used post-larval carapace length as an approximation of CL_h. In the present study, CL_h was estimated as 3 mm, since Nurse (1980) found that carapace length of the final larval stage of *T. australiensis* at Gray's Point in Port Hacking, ranged between 2.6 mm and 2.9 mm.

Longevity was calculated from Pauly's (1984) equation: t_{max} = 3/k. Growth performance index (phi-prime index) φ' was calculated from Pauly and Munro's (1984) equation:

$$\varphi' = \log_{10} k + 2 \log_{10} L_\infty$$

Natural mortality (M) was estimated by the empirical formula of Pauly (1980), contained within FiSAT II, using mean annual water temperatures from each site. The reliability of M was established using the M/K ratio, which has been reported to be within the range of 1.12 - 2.5 for most fishes (Beverton and Holt, 1966). Total mortality rates (Z) were derived from length converted catch curves (Sparre *et al.*, 1989) and also calculated by FiSAT II (Gayanilo *et al.*, 1995). Fishing mortality rates (F) were calculated as Z - M. Exploitation ratio (E) was computed from: $E = F/Z$ (Ricker, 1975) and is defined as the fraction of mortality caused by fishing.

5.3. Results

5.3.1 Relative growth

Total length was linearly related to carapace length for both males and females across all sites (Fig. 5.1, Tables 5.1 - 5.5). REGRANS revealed transition points for all data sets and separate regressions were fitted to data above and below these points (Tables 5.1 - 5.5). Growth was positively allometric below transition points across all sites and sexes, with total length increasing more rapidly than CL (Table 5.6). Beyond transition points, growth became negatively allometric, with CL increasing faster than total length. There were significant differences between males and females for upper and lower regression lines at most sites, as well as between regressions for total data sets (ANCOVA, $P < 0.05$; Tables 5.1 - 5.5). In general, females attained a greater total length than males of the same carapace length.

Chela height (ChH) was linearly related to carapace length (Fig. 5.2). Transition points were calculated by REGRANS and accepted for all sites and sexes apart from females at Garlandtown, as there was no significant difference between the sum of the squared residuals for the data as a whole, against the sum of the squared residuals for lines to the left and right of the transition points. Therefore, only one regression line was fitted to the data set (Fig. 5.2, Table 5.4). Transition points identified by REGRANS in the analysis of chela height (ChH) against carapace length identify sexual maturation. Size at maturity was significantly related to latitude for both males ($R^2 = 0.99$, $F = 293.02$, $P < 0.0001$, n = 5) and

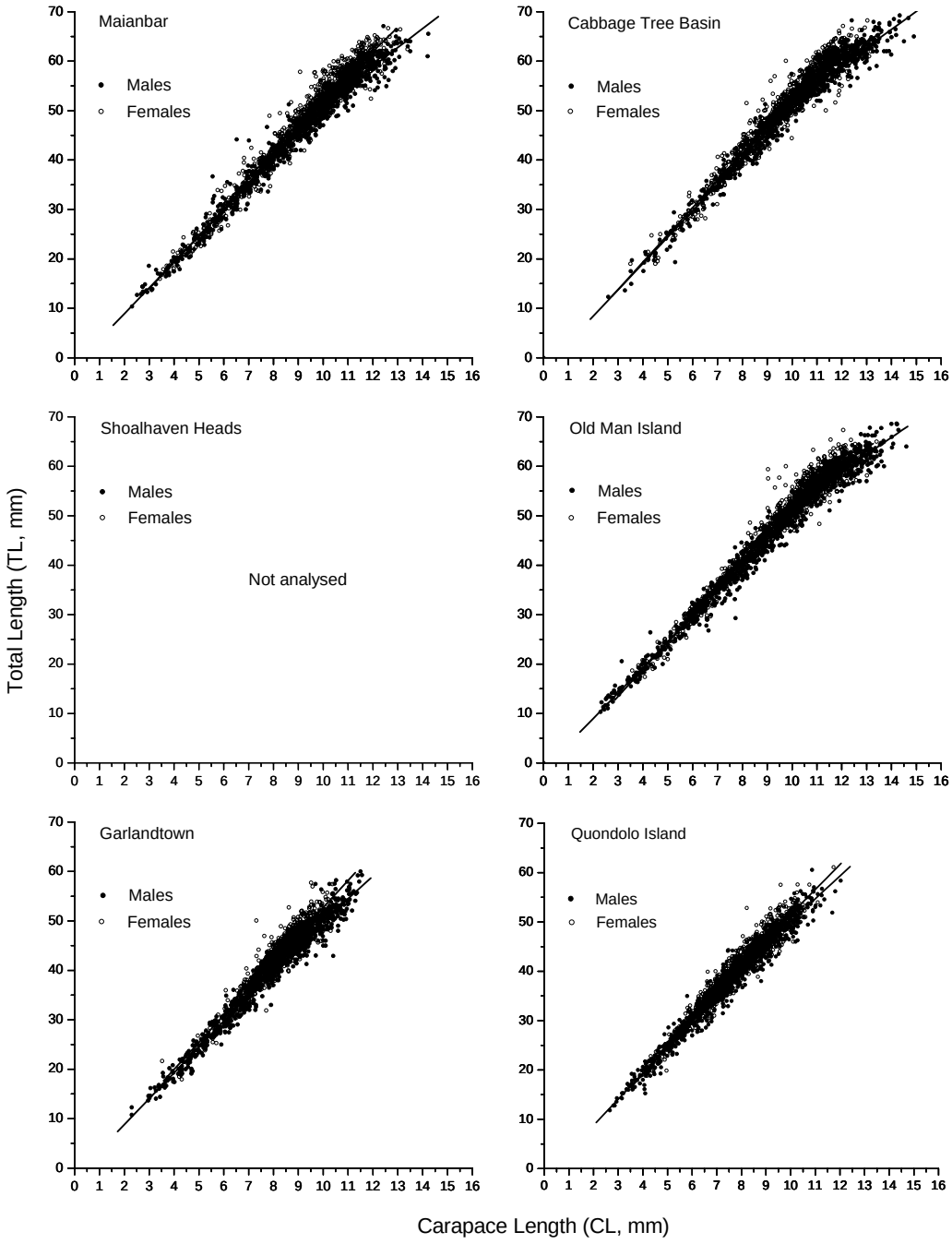


Figure 5.1. Regressions of total length (TL) on carapace length (CL) (untransformed data) for male and female *T. australiensis* at Maianbar, Cabbage Tree Basin, Old Man Island, Garlandtown and Quondolo Island between January 2001 and January 2003. Shoalhaven Heads not analysed due to absence of small individuals. See Tables 5.1 - 5.6 for regression equations, location of transition points and allometric coefficients.

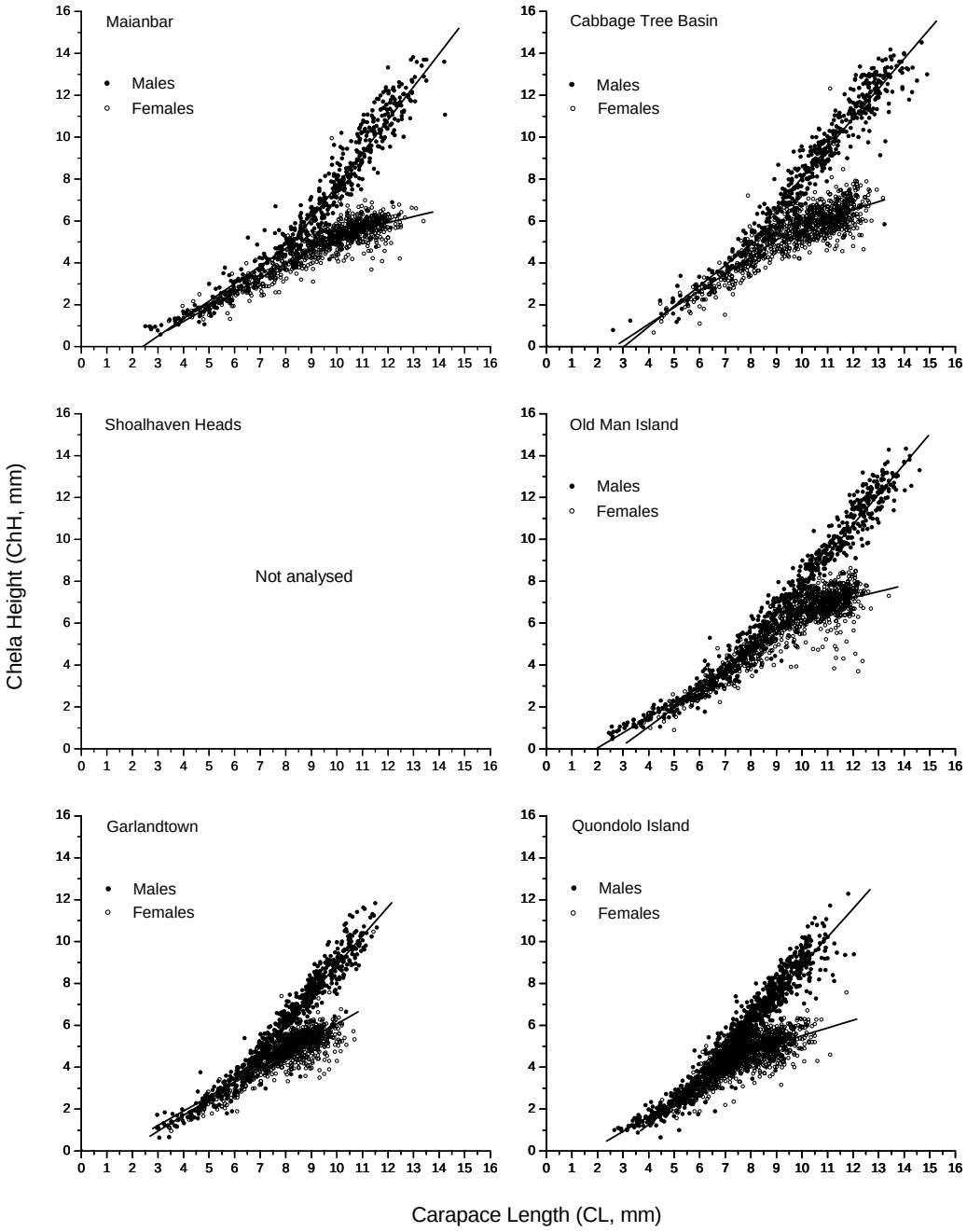


Figure 5.2. Regressions of chela height (ChH) on carapace length (CL) (untransformed data) for male and female *T. australiensis* at Maianbar, Cabbage Tree Basin, Old Man Island, Garlandtown and Quondolo Island between January 2001 and January 2003. Shoalhaven Heads not analysed due to absence of small individuals. See Tables 5.1 - 5.6 for regression equations, location of transition points and allometric coefficients.

Table 5.1. Least squares regressions (untransformed data) of total length (TL) on carapace length (CL), chela height (ChH) on carapace length (CL), chela width (ChW) on carapace length (CL), chela height (ChH) on chela width (ChW) and multiplicative relationship ($y = ax^b$) of wet weight (WW) on carapace length (CL) for males and females of *T. australiensis* at Maianbar between January 2001 and January 2003. Data were subdivided at transition points X as determined by REGRANS, yielding separate regressions for data points ≤X and ≥X. NA = transition point not applicable and data explained by single regression. R^2 = coefficient of determination. $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***). Slopes and intercepts with the same superscript are significantly different ($P < 0.05$) for selected comparisons using ANCOVA (see text).

		Lower Line ≤X				Upper Line ≥X				Total data set			
Maianbar	X	Intercept	Slope	d.f	R^2	Intercept	Slope	d.f	R^2	Intercept	Slope	d.f	R^2
Males													
TL:CL	9.89	-1.55^{a}	5.23^{b}	441	0.96***	13.08^{g}	$3.81^{b,h}$	328	0.76***	0.40^{d}	$4.95^{b,c}$	771	0.97***
ChH:CL	8.53	-1.98^{n}	$0.83^{i,o}$	188	0.87***	-8.17^{p}	$1.59^{i,q}$	361	0.85***	-4.68^{j}	$1.26^{i,k}$	551	0.92***
ChW:CL	na									-3.05^{r}	1.17^{s}	554	0.92***
ChH:ChW	6.52	0.53^{y}	$1.13^{t,z}$	248	0.93***	3.06^{α}	$0.73^{t,\beta}$	297	0.83***	1.51^{u}	$0.90^{t,v}$	547	0.95***
WW:CL	na									-3.06^{γ}	3.33	771	0.95***
Females													
TL:CL	8.02	-1.34^{e}	5.25	193	0.91***	3.45^{g}	$4.87^{f,h}$	802	0.85***	$-1.17^{d,e}$	$5.31^{e,f}$	997	0.96***
ChH:CL	9.8	$-1.54^{l,n}$	$0.69^{m,o}$	369	0.84***	$2.57^{l,p}$	$0.28^{m,q}$	468	0.10***	-0.71^{j}	$0.58^{k,m}$	839	0.79***
ChW:CL	na									-0.78^{r}	0.77^{s}	845	0.70***
ChH:ChW	4.85	$0.24^{w,y}$	$1.32^{x,z}$	316	0.87***	$2.35^{w,\alpha}$	$0.92^{x,\beta}$	526	0.73***	$0.90^{u,w}$	$1.16^{v,x}$	844	0.89***
WW:CL	na									-2.94^{γ}	3.21	1188	0.94***

Table 5.2. Least squares regressions (untransformed data) of total length (TL) on carapace length (CL), chela height (ChH) on carapace length (CL), chela width (ChW) on carapace length (CL), chela height (ChH) on chela width (ChW) and multiplicative relationship ($y = ax^b$) of wet weight (WW) on carapace length (CL) for males and females of *T. australiensis* at Cabbage Tree Basin (CTB) between January 2001 and January 2003. Data were subdivided at transition points X as determined by REGRANS, yielding separate regressions for data points ≤X and ≥X. NA = transition point not applicable and data explained by single regression. R^2 = coefficient of determination. $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***). Slopes and intercepts with the same superscript are significantly different ($P < 0.05$) for selected comparisons using ANCOVA (see text).

		Lower Line ≤X				Upper Line ≥X				Total data set			
CTB	X	Intercept	Slope	d.f	R^2	Intercept	Slope	d.f	R^2	Intercept	Slope	d.f	R^2
Males													
TL:CL	9.84	-2.46^{f}	5.36^{a}	301	0.96***	15.39^{g}	$3.64^{a,h}$	369	0.84***	2.50^{c}	$4.73^{a,b}$	670	0.96***
ChH:CL	8.89	$-2.96^{i,k,t}$	$0.98^{j,l,u}$	140	0.83***	$-6.13^{i,v}$	$1.42^{j,w}$	397	0.84***	$-5.87^{k,m}$	$1.39^{l,n}$	537	0.93***
ChW:CL	11.9	-3.69^{x}	1.24^{y}	382	0.91***	6.95^{x}	0.37^{y}	153	0.05**	-2.79^{z}	$1.14^{y,\alpha}$	537	0.90***
ChH:ChW	6.01	0.60^{β}	1.12^{γ}	137	0.90***	$3.47^{\beta,\delta}$	0.68^{γ}	400	0.84***	$6.01^{\delta,\varepsilon}$	$2.13^{\gamma,\zeta}$	539	0.93***
WW:CL	na									-3.06^{ι}	3.33κ	771	0.95***
Females													
TL:CL	11.02	$-2.75^{d,f}$	5.52^{e}	666	0.95***	28.6^{g}	$2.71^{e,h}$	327	0.23***	$0.06^{c,d}$	$5.19^{b,e}$	995	0.94***
ChH:CL	9.99	$-2.37^{o,q,t}$	$0.83^{p,r,u}$	356	0.76***	$1.96^{q,s,v}$	$0.38^{r,w}$	472	0.10***	$-0.82^{m,o,s}$	$0.64^{n,p}$	830	0.68***
ChW:CL	na									-0.78^{z}	0.77^{α}	845	0.70***
ChH:ChW	5.79	0.46^{η}	1.24^{θ}	416	0.87***	3.97	0.62^{θ}	414	0.34***	$1.31^{\varepsilon,\eta}$	$1.04^{\zeta,\theta}$	832	0.85***
WW:CL	na									-2.94^{ι}	3.21^{κ}	1188	0.94***

Table 5.3. Least squares regressions (untransformed data) of total length (TL) on carapace length (CL), chela height (ChH) on carapace length (CL), chela width (ChW) on carapace length (CL), chela height (ChH) on chela width (ChW) and multiplicative relationship ($y = ax^b$) of wet weight (WW) on carapace length (CL) for males and females of *T. australiensis* at Old Man Island between January 2001 and January 2003. Data were subdivided at transition points X as determined by REGRANS, yielding separate regressions for data points ≤X and ≥X. NA = transition point not applicable and data explained by single regression. R^2 = coefficient of determination. $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***). Slopes and intercepts with the same superscript are significantly different ($P < 0.05$) for selected comparisons using ANCOVA (see text).

		Lower Line ≤X				Upper Line ≥X				Total data set			
Old Man Island	X	Intercept	Slope	d.f	R^2	Intercept	Slope	d.f	R^2	Intercept	Slope	d.f	R^2
Males													
TL:CL	10.59	$-1.22^{a,c,h}$	$5.14^{b,i}$	682	0.94***	$17.84^{a,j}$	3.43^{b}	314	0.72***	$0.76^{c,d}$	$4.86^{b,e}$	998	0.96***
ChH:CL	7.58	-1.00^{k}	$0.66^{l,p}$	204	0.48***	$-6.48^{k,q}$	$1.43^{l,r}$	521	0.90***	-4.45^{m}	$1.24^{l,n}$	727	0.92***
ChW:CL	9.83	$-2.21^{s,y}$	1.06^{t}	392	0.80***	$0.59^{s,z}$	$0.85^{t,\alpha}$	332	0.40***	-2.40^{u}	$1.10^{t,v}$	726	0.89***
ChH:ChW	7.77	$0.83^{\beta,\iota}$	$1.07^{\gamma,\delta,\kappa}$	408	0.88***	$4.37^{\beta,\varepsilon}$	0.60^{γ}	316	0.43***	$1.71^{\varepsilon,\zeta}$	$0.86^{\delta,\eta}$	726	0.90***
WW:CL	na									-3.10^{λ}	3.35	998	0.96***
Females													
TL:CL	10.51	$-3.39^{f,h}$	$5.52^{g,i}$	516	0.90***	$19.51^{f,j}$	3.40^{g}	480	0.41***	-0.84^{d}	$5.21^{e,g}$	998	0.92***
ChH:CL	9.86	-2.52	$0.89^{o,p}$	379	0.88***	3.69^{q}	$0.29^{o,r}$	577	0.08***	-1.50^{m}	$0.76^{n,o}$	958	0.83***
ChW:CL	10.43	$-2.61^{w,y}$	1.08^{x}	494	0.90***	$6.33^{w,z}$	$0.19^{x,\alpha}$	462	0.01*	$-0.84^{u,w}$	$0.85^{v,x}$	958	0.78***
ChH:ChW	6.05	0.40^{ι}	$1.22^{\theta,\kappa}$	348	0.94***	3.51	0.72^{θ}	3348	0.94***	0.96^{ζ}	$1.08^{\eta,\theta}$	960	0.90***
WW:CL	na									-2.98^{λ}	3.25	956	0.94***

Table 5.4. Least squares regressions (untransformed data) of total length (TL) on carapace length (CL), chela height (ChH) on carapace length (CL), chela width (ChW) on carapace length (CL), chela height (ChH) on chela width (ChW) and multiplicative relationship ($y = ax^b$) of wet weight (WW) on carapace length (CL) for males and females of *T. australiensis* at Garlandtown between January 2001 and January 2003. Data were subdivided at transition points X as determined by REGRANS, yielding separate regressions for data points ≤X and ≥X. NA = transition point not applicable and data explained by single regression. R^2 = coefficient of determination. $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***). Slopes and intercepts with the same superscript are significantly different ($P < 0.05$) for selected comparisons using ANCOVA (see text).

		Lower Line ≤X				Upper Line ≥X				Total data set			
Garlandtown	X	Intercept	Slope	d.f	R^2	Intercept	Slope	d.f	R^2	Intercept	Slope	d.f	R^2
Males													
TL:CL	8.01	-1.68	5.24^{a}	394	0.90***	4.89	$4.50^{a,b}$	452	0.81***	-0.78^{c}	$5.10^{b,d}$	848	0.95***
ChH:CL	5.70	-1.33^{e}	0.76^{f}	82	0.73***	-5.24^{e}	1.41^{f}	525	0.88***	$-4.04^{e,g}$	$1.28^{f,h}$	609	0.91***
ChW:CL	na									-2.50^{k}	1.19^{l}	612	0.92***
ChH:ChW	6.95	$0.90^{m,t}$	$1.04^{n,o,u}$	347	0.89***	3.16^{m}	$0.69^{n,v}$	260	0.68***	$1.49^{m,p}$	$0.90^{o,q}$	609	0.93***
WW:CL	na									-3.26^{w}	3.58^{x}	604	0.95***
Females													
TL:CL	na									-1.86^{c}	5.46^{d}	998	0.84***
ChH:CL	na									-0.86^{g}	0.69^{h}	883	0.68***
ChW:CL	8.50	-2.31^{i}	1.08^{j}	511	0.74***	3.79^{i}	0.34^{j}	371	0.06***	$-0.43^{i,k}$	$0.82^{j,l}$	884	0.65***
ChH:ChW	5.26	$0.46^{r,t}$	$1.22^{s,u}$	586	0.80***	4.60^{r}	$0.45^{s,v}$	296	0.17***	1.11^{p}	$1.07^{q,s}$	884	0.78***
WW:CL	na									-3.15^{w}	3.46^{x}	879	0.89***

Table 5.5. Least squares regressions (untransformed data) of total length (TL) on carapace length (CL), chela height (ChH) on carapace length (CL), chela width (ChW) on carapace length (CL), chela height (ChH) on chela width (ChW) and multiplicative relationship ($y=ax^b$) of wet weight (WW) on carapace length (CL) for males and females of *T. australiensis* at Quondolo Island between January 2001 and January 2003. Data were subdivided at transition points X as determined by REGRANS, yielding separate regressions for data points <X and ≥X. NA = transition point not applicable and data explained by single regression. R^2 = coefficient of determination. $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***). Slopes and intercepts with the same superscript are significantly different ($P < 0.05$) for selected comparisons using ANCOVA (see text).

		Lower Line ≤X				Upper Line ≥X				Total data set			
Quondolo Island	X	Intercept	Slope	d.f	R^2	Intercept	Slope	d.f	R^2	Intercept	Slope	d.f	R^2
Males													
TL:CL	8.20	-1.77^{g}	$5.29^{a,h}$	579	0.91***	5.77^{i}	$4.42^{a,j}$	395	0.77***	-0.63^{b}	$5.10^{a,c}$	976	0.95***
ChH:CL	5.70	-1.18^{k}	$0.70^{l,r}$	171	0.71***	$-4.77^{k,s}$	$1.36^{l,t}$	803	0.86***	-3.91^{m}	$1.26^{l,n}$	976	0.91***
ChW:CL	na									-2.77^{u}	1.23^{v}	976	0.90***
ChH:ChW	5.14	$0.42^{z,\theta}$	1.17^{α}	415	0.91***	$2.46^{z,\beta,\iota}$	0.79^{α}	559	0.80***	$1.17^{\beta,\gamma}$	$0.96^{\alpha,\delta}$	976	0.94***
WW:CL	na									-3.13^{κ}	3.45	970	0.93***
Females													
TL:CL	8.65	$-3.42^{d,g}$	$5.64^{e,f,h}$	731	0.89***	$0.90^{d,i}$	$5.06^{e,j}$	265	0.62***	$-1.45^{b,d}$	$5.35^{e,f}$	998	0.92***
ChH:CL	7.73	$-2.53^{o,q}$	$0.95^{p,r}$	479	0.72***	$1.79^{o,s}$	$0.37^{p,t}$	517	0.18***	$-0.43^{m,q}$	$0.63^{n,p}$	998	0.66***
ChW:CL	8.07	$-2.48^{w,y}$	1.12^{x}	582	0.72***	1.73^{w}	0.55^{x}	414	0.20***	$-0.33^{u,y}$	$0.80^{v,x}$	998	0.68***
ChH:ChW	5.26	$0.44^{\varepsilon,\theta}$	1.23^{ζ}	799	0.85***	$2.47^{\varepsilon,\eta,\iota}$	0.83^{ζ}	197	0.26***	$0.71^{\gamma,\eta}$	$1.16^{\delta,\zeta}$	998	0.86***
WW:CL	na									-2.97^{κ}	3.25	998	0.89***

females (R^2 = 0.81, F = 13.52, P < 0.05, n = 4), with individuals from southern locations maturing at smaller sizes than northern populations (Fig. 5.3). Before maturity, relative growth of chela height (ChH) and CL was positively allometric for both sexes across all sites (Table 5.6). Beyond maturation, relative growth became increasingly positively allometric for males and negatively allometric for females. Female size at maturity was analysed in Chapter 4, based on the presence of ovigerous females. The transition points calculated by REGRANS for females are between the smallest ovigerous female and mean size of ovigerous females, estimated in Chapter 4 (Table 5.7). ANCOVA revealed significant differences (P < 0.05) in slopes and intercepts between upper and lower lines of males and females respectively at most sites, as well as between upper and lower lines and total data sets (Tables 5.1 - 5.5).

The difference in allometric growth between males and females results in sexual dimorphism, with males possessing a larger, differently shaped primary chela. Sexual dimorphism was evident in regressions of chela height (ChH) against chela width (ChW) and transition points identified by REGRANS indicate changes in shape before and after maturation (Fig. 5.4). Although growth of ChH in relation to ChW was similar for both sexes, that is, negatively allometric to increasingly negatively allometric (Table 5.6), chela height (ChH) in females stopped increasing following sexual maturity (Fig. 5.4). The sizes at which ChH stopped increasing in relation to ChW in females corresponded well to the maturation points estimated in regressions of CL and ChH by REGRANS. ANCOVA frequently revealed significant differences between upper and lower

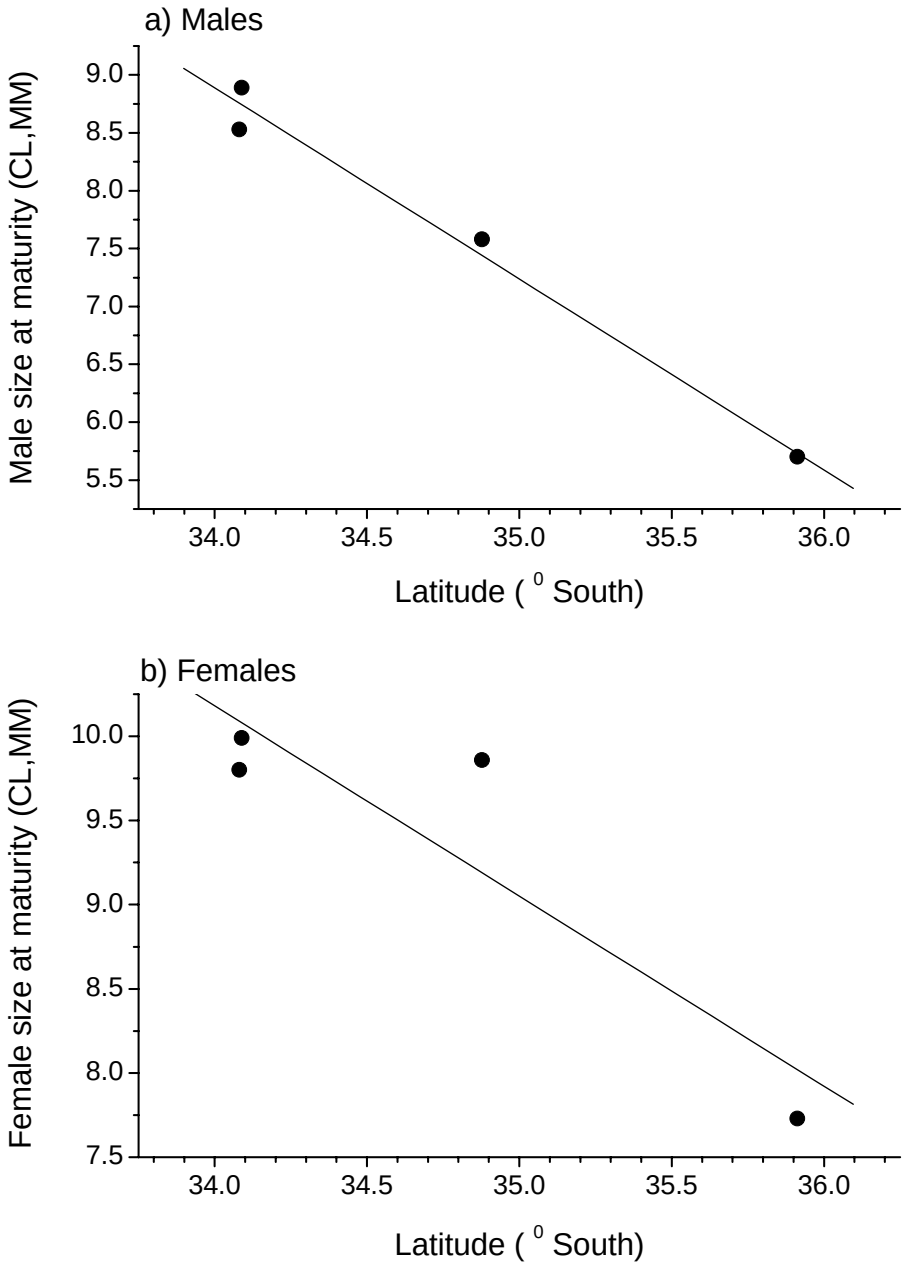


Figure 5.3. Relationship between (a) Male size at maturity (determined by REGRANS) and latitude for each population of *T. australiensis* (Shoalhaven Heads excluded), combined for all sampling occasions between January 2001 and February 2003. (b) Female size at maturity (determined by REGRANS) and latitude for each population of *T. australiensis* (Shoalhaven Heads and Garlandtown excluded), combined for all sampling occasions between January 2001 and February 2003. See text for equations.

Table 5.6. Allometric coefficients expressed as slopes of *log*-transformed least squares regressions of total length (TL) on carapace length (CL), chela height (ChH) on carapace length (CL), chela height on chela width (ChW) and chela width (ChW) on carapace length (CL) for males and females of *T. australiensis* at Maianbar, Cabbage Tree Basin, Old Man Island, Garlandtown and Quondolo Island between January 2001 and January 2003. Data were subdivided at transition points X as determined by REGRANS, yielding separate regressions for data points <X and ≥X. 95% CI = confidence interval of allometric coefficient.

Site	TL:CL Allom. coef	95% CI	ChH:CL Allom. coef	95% CI	ChH:ChW Allom. coef	95% CI	ChW:CL Allom. coef	95% CI
1) Maianbar								
Males								
Total data set	1.02**	±0.01	1.8738***	±0.03	0.82***	±0.01	1.55***	±0.03
≤X	1.06***	±0.02	1.7089***	±0.08	0.89***	±0.03	-	-
≥X	0.78***	±0.05	1.9776***	±0.09	0.69***	±0.03	-	-
Females								
Total data set	1.04***	±0.01	1.29***	±0.04	0.92***	±0.02	1.25***	±0.04
≤X	1.05*	±0.04	1.49***	±0.06	0.94**	±0.03	-	-
≥X	0.95***	±0.02	0.58***	±0.14	0.69***	±0.03	-	-
2) Cabbage Tree Basin								
Males								
Total data set	0.99	±0.01	1.92***	±0.04	0.89***	±0.05	1.50***	±0.04
≤X	1.08***	±0.02	1.82***	±0.11	0.65***	±0.03	1.65***	±0.04
≥X	0.74***	±0.03	1.68***	±0.08	0.77***	±0.01	0.40***	±0.29
Females								
Total data set	1.03***	±0.01	1.34***	±0.05	0.84***	±0.03	1.08**	±0.05
≤X	1.08***	±0.02	1.68***	±0.10	0.89***	±0.03	-	-
≥X	0.55***	±0.11	0.66***	±0.18	0.84***	±0.02	-	-
3) Old Man Island								
Males								
Total data set	1.01	±0.02	1.83***	±0.04	0.77***	±0.02	1.46***	±0.04
≤X	1.04*	±0.03	1.60***	±0.16	0.81***	±0.04	1.53***	±0.06
≥X	0.70***	±0.05	1.43***	±0.02	0.56***	±0.15	0.87	±0.24
Females								
Total data set	1.05***	±0.03	1.46***	±0.03	0.88***	±0.02	1.30***	±0.04
≤X	1.09***	±0.05	1.70***	±0.06	0.94***	±0.02	1.57***	±0.04
≥X	0.68***	±0.07	0.44***	±0.14	0.60***	±0.14	0.23***	±0.07
4) Garlandtown								
Males								
Total data set	1.04***	±0.02	1.86***	±0.05	0.77***	±0.02	1.52***	±0.04
≤X	1.05	±0.03	1.69***	±0.22	0.83***	±0.03	-	-
≥X	0.90***	±0.04	1.90***	±0.08	0.66***	±0.06	-	-
Females								
Total data set	1.07**	±0.04	1.37***	±0.05	0.86***	±0.04	1.25***	±0.05
≤X	-	-	-	-	0.91***	±0.05	1.53***	±0.10
≥X	-	-	-	-	0.39***	±0.10	0.43***	±0.20
5) Quondolo Island								
Males								
Total data set	1.04***	±0.02	1.89***	±0.03	0.84***	±0.01	1.61***	±0.03
≤X	1.06***	±0.04	1.58***	±0.16	0.90***	±0.02	-	-
≥X	0.89***	±0.05	1.85***	±0.06	0.71***	±0.03	-	-
Females								
Total data set	1.06***	±0.03	1.26***	±0.04	0.89***	±0.02	1.20***	±0.05
≤X	1.11***	±0.04	1.81***	±0.08	0.92***	±0.03	1.61***	±0.07
≥X	0.99	±0.10	0.64***	±0.11	0.65***	±0.18	0.75**	±0.16

regression lines of males versus females as well as between regressions of total data sets within sexes (Tables 5.1 - 5.5).

No clear patterns were evident in regressions of carapace length and chela width (ChW) by REGRANS. Transition points could not be accepted for many sites and single regressions were used to describe these data. For simplicity, relationships between carapace length and chela width (ChW) have not been shown graphically, although equations, results of ANCOVA and allometric growth coefficients are presented in Tables 5.1 to 5.6. ANCOVA revealed significant differences between the slopes and intercepts of the total data sets of males and females and the relationship between CL and ChW was significantly positively allometric across all sites.

Table 5.7. Sizes at maturity (CL, mm) of males and females determined by relative growth analyses (REGRANS) compared to reproductive condition (minimum and mean size of ovigerous females) for each site (Maianbar, Cabbage Tree Basin, Shoalhaven Heads, Old Man Island, Garlandtown and Quondolo Island) estuary (Port Hacking, Shoalhaven and Moruya), between January 2001 and February 2003. Standard errors shown in parentheses. Hyphen indicates that analyses were not performed or transition points could not be accepted (see text).

Site	REGRANS Males	REGRANS Females	Minimum ovigerous	Mean ovigerous
Maianbar	8.53	9.8	8.03	10.32 (0.08)
Cabbage Tree Basin	8.89	9.99	7.29	10.82 (0.08)
Shoalhaven Heads	-	-	8.34	11.12 (0.11)
Old Man Island	7.58	9.86	6.11	10.73 (0.09)
Garlandtown	5.7	-	5.77	8.54 (0.06)
Quondolo Island	5.7	7.73	5.41	8.27 (0.06)

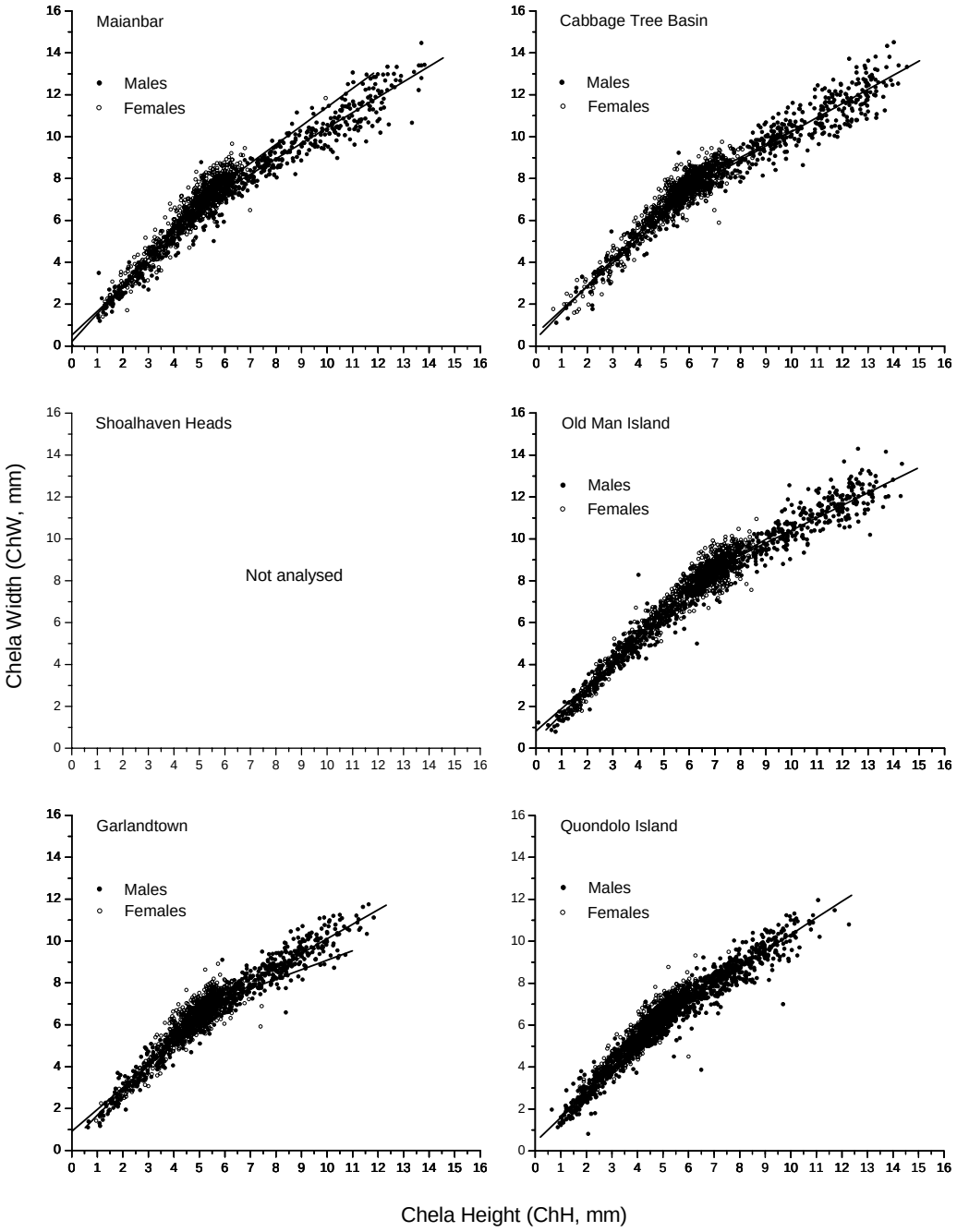


Figure 5.4. Regressions of chela width (ChW) on chela height (ChH) (untransformed data) for male and female *T. australiensis* at Maianbar, Cabbage Tree Basin, Old Man Island, Garlandtown and Quondolo Island between January 2001 and January 2003. Shoalhaven Heads not analysed due to absence of small individuals. See Tables 5.1 - 5.6 for regression equations, location of transition points and allometric coefficients.

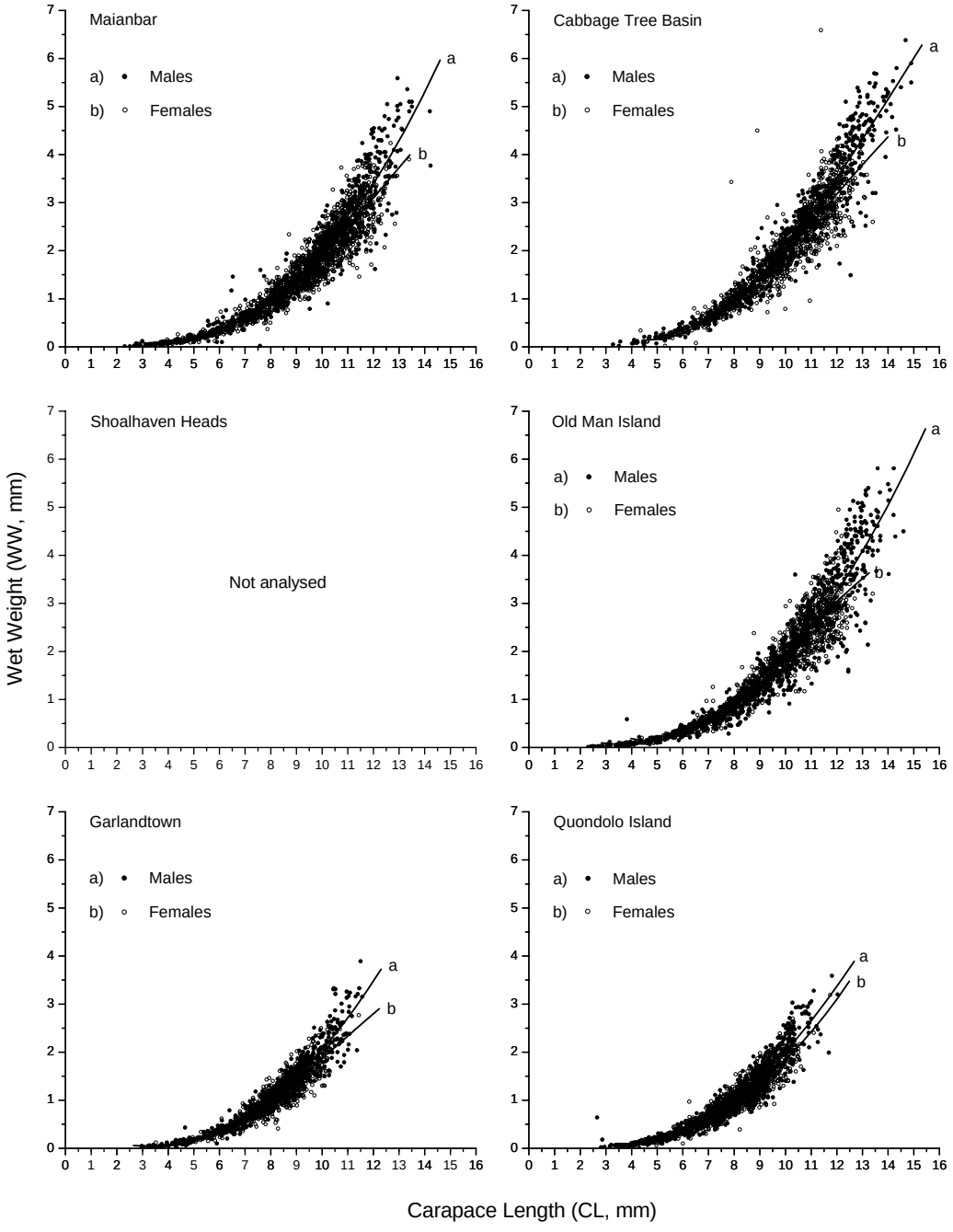


Figure 5.5. Regressions of wet weight (WW) on carapace length (CL) (untransformed data) for male and female *T. australiensis* at Maianbar, Cabbage Tree Basin, Old Man Island, Garlandtown and Quondolo Island between January 2001 and January 2003. Shoalhaven Heads not analysed due to absence of small individuals. See Tables 5.1 - 5.6 for regression equations, and allometric coefficients.

Carapace length was related to wet weight by approximately the third power for all sites and sexes (Tables 5.1 - 5.5), indicating that relative growth was isometric. Significant differences between slopes and intercepts revealed by ANCOVA for the relationship between carapace length and wet weight for males and females were not consistent between sites. It was evident that slopes were greater for males, indicating that males were heavier than females of the same carapace length.

There were no obvious patterns in the ratio of left:right handed individuals between sites or sex (Table 5.8). Although the ratio often fluctuated between left and right-handed individuals through time, significant differences due to sex were uncommon. With sexes combined, differences were even less frequent, with the ratio between left and right-handed individuals significantly different on only 5 occasions. For some sites such as Shoalhaven Heads and Quondolo Island, chela ratio was never significantly different.

Table 5.8. Primary chela ratio (left/right) of *T. australiensis* for males, females and combined data (both) at Maianbar (MB), Cabbage Tree Basin (CTB), Shoalhaven Heads (SHH), Old Man Island (OMI), Garlandtown (GT) and Quondolo Island (QI) between January 2001 and January 2003. Asterisks indicate ratios significantly different from 1:1 (χ^2). $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***).

	Primary chela ratio (left/right)																	
Site	**MB**			**CTB**			**SHH**			**OMI**			**GT**			**QI**		
	M	F	Both	M	F	Both	M	F	Both	M	F	Both	M	F	Both	M	F	Both
Month/Year																		
Jan 01	0.83	0.58	0.69	1.54	1.35	1.29	1.75	0.60	0.84	0.70	1.16	0.92	0.69	1.13	0.87	0.97	0.86	0.91
Feb	0.68	0.62	0.65*	0.67	1.85*	1.34	1.50	0.92	1.05	1.15	0.87	0.97	0.60	0.93	0.79	0.83	0.98	0.92
March	1.27	0.93	1.04	0.83	1.2	1.02	1.57	1.21	1.33	0.82	1.73	1.30	0.93	1.14	1.05	0.90	1.11	1.04
May	1.31	0.81	0.98	0.74	0.76	0.75	0.50	1.11	0.76	0.45**	1.00	0.73	1.14	0.92	0.97	0.77	0.93	0.85
Jun	0.68	0.83	0.76	1	1.2	1.11	2.30	0.60	1.00	0.97	0.84	0.89	1.28	0.54*	0.78	1.28	0.82	1.01
July	0.90	0.96	0.93	0.83	0.87	0.85	0.44	0.75	0.64	0.96	1.02	1.00	0.68	0.57*	0.61*	0.93	0.96	0.96
Aug	0.60	0.89	0.79	0.83	1.00	1.00	0.70	0.73	0.72	0.91	0.69	0.77	0.60	1.03	0.81	1.04	0.86	0.92
Sep	1.00	1.27	1.20	1.44	0.79	0.96	1.00	1.00	1.00	0.85	0.96	0.91	0.94	0.83	0.87	1.08	1.0	1.04
Oct	1.14	0.79	0.93	1.1	0.94	1.00	1.12	1.66	1.43	1.14	0.79	0.95	1.53	0.85	1.03	0.96	0.95	0.96
Nov	0.96	0.82	0.88	1.41	1.05	1.14	1.21	1.00	1.08	1.12	1.02	1.06	1.07	1.02	1.04	0.85	1.19	1.02
Dec	1.27	0.77	0.95	1.61	1.02	1.22	1.62	0.82	0.98	0.95	1.00	0.98	1.40	1.02	1.16	0.85	1.12	1.00
Jan 02	0.87	1.36	1.11	1.42	1.44	1.43*	1.00	1.08	1.05	2.17**	1.26	1.57**	1.06	0.74	0.85	1.09	0.83	0.94
Mar	0.96	0.74	0.80															
Apr	1.59	0.86	1.10															
Jun	1.05	1.09	1.08															
Jul	1.33	0.79	0.96	0.53*	1.38	0.95	1.67	1.28	1.40	0.88	0.82	0.85	1.22	1.22	1.22	0.81	1.27	1.07
Aug	1.23	1.17	1.19															
Sep	0.96	1.25	1.10															
Oct	0.70	1.08	0.93	1.55	1	1.18	0.75	1.00	0.92	0.76	0.76	0.76	1.18	0.87	1.00	0.73	1.06	0.89
Nov	1.06	1.07	1.07															
Dec	1.00	1.51	1.30															
Jan 03	0.90	1.18	1.05	1.03	1.32	1.21	1.4	0.92	1.06	1.00	1.07	1.03	0.80	0.82	0.83	0.75	0.79	0.75*
All samples	1.01	0.96	0.98	1.09	1.10	1.10	1.10	0.96	1.00	0.97	0.96	0.96	1.00	0.88*	0.93	0.97	0.98	0.95

5.3.2 Absolute growth

Parameters calculated from the von Bertalanffy growth function (VBGF) for each site as estimated by ELEFAN are summarised in Table 5.9. Values of L_∞ and k varied across sites and ranged between 12.60 - 15.75 mm and 0.37 - 0.98 year^{-1} respectively. Despite being almost identical for sites in the Moruya River, these parameters differed markedly between sites within Port Hacking and the Shoalhaven River. In particular, the low k values at Maianbar and Old Man Island were not consistent with higher growth rates at other sites and estuaries. VBGF growth curves fitted to length frequency distributions are given in Figures 5.6 to 5.8. ELEFAN identified 3 to 5 cohorts across most sites, although in many cases curves missed some peaks in the length data, which is reflected by generally low *Rn* (goodness of fit index) values. In fact, for Maianbar and Old Man Island, multiple curves were fitted through what appeared to be single cohorts, as well as through regions which contained no data. Since ELEFAN cannot produce t_0 estimates from size frequency distributions, adjusted growth curves were also produced using values of t_0 calculated according to Lopez Veiga (1979) and are shown in Figure 5.10.

Longevity was less than 4 years across most sites, although at sites with low k values such as Maianbar and Cabbage Tree Basin, t_{max} values as high as 6 years and 8.11 years respectively were calculated (Table 5.9). Growth performance indices (φ') ranged from 1.90 to 2.38 and no consistent patterns were evident between sites or estuaries. Natural mortality (M) estimates ranged from 1.21 - 1.82 yr-^{1} and most reliability ratios (M/K) were all within an acceptable range of 1.12 - 2.5 (Beverton and Holt, 1959), apart from Old Man Island (Table 5.9). The

average instantaneous total mortality rate (*Z)*, calculated from length-converted catch curves (Fig. 5.9) ranged from 1.18 - 3.76 yr^{-1} (Table 5.9). Fishing mortality (*F*), estimated from *Z* - *M*, was between 0.23 $^{yr-1}$ and 0.94 yr^{-1} across all sites (Table 5.9). Exploitation ratios (*E*) were all lower than the expected optimal level (E_{opt} = 0.5) except for Cabbage Tree Basin, which had a value of 0.52 (Table 5.9).

Table 5.9. Growth parameters of *T. australiensis*, combined for males and females at Maianbar (MB), Cabbage Tree Basin (CTB), Shoalhaven Heads (SHH), Old Man Island (OMI), Garlandtown (GT) and Quondolo Island (QI) between January 2001 and January 2003. See text for definitions.

Parameters	**MB**	**CTB**	**SHH**	**OMI**	**GT**	**QI**
L_∞	14.7	15.75	15.75	14.70	12.60	12.60
K ($year^{-1}$)	0.5	0.97	0.98	0.37	0.82	0.78
t_0 (years)	-0.45	-0.22	-0.22	-0.61	-0.33	-0.35
t_{max} (years)	6	3.09	3.06	8.11	3.66	3.85
φ	2.03	2.38	2.38	1.90	2.11	2.09
Mean temp (°C)	21.08	20.80	19.43	19.13	19.71	19.81
M ($year^{-1}$)	1.21	1.82	1.78	0.95	1.70	1.64
M/*K*	2.42	1.88	1.81	2.57	2.07	2.10
F ($year^{-1}$)	0.94	1.94	1.23	0.23	1.40	1.55
Z ($year^{-1}$)	2.15	3.76	3.01	1.18	3.10	3.20
E = *F*/*Z*	0.44	0.52	0.41	0.19	0.45	0.48

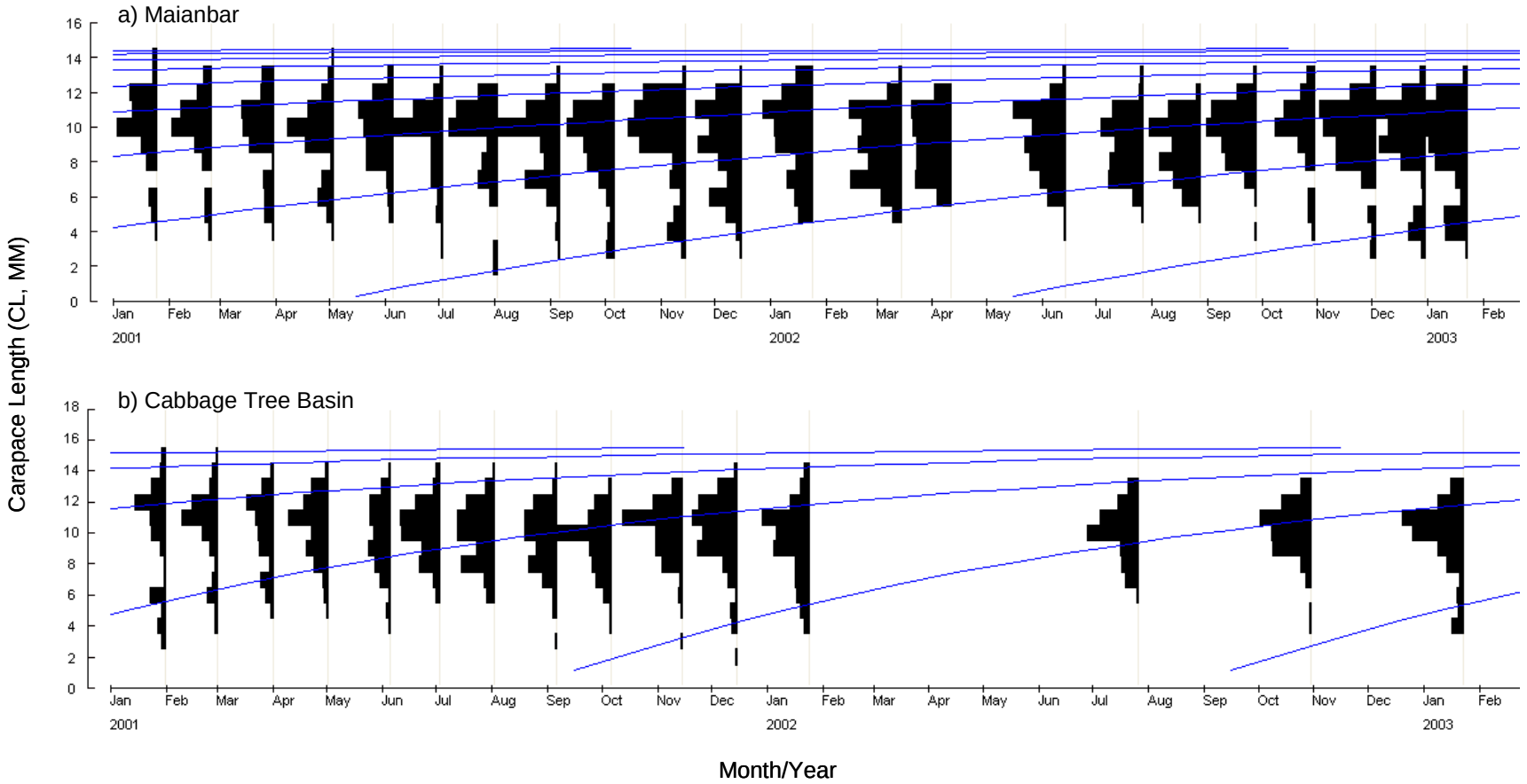


Figure 5.6. Length frequency distributions (CL, MM) and growth curves for *T. australiensis* at a) Maianbar and b) Cabbage Tree Basin in Port Hacking between January 2001 and January 2003. See Table 5.9 for growth parameters.

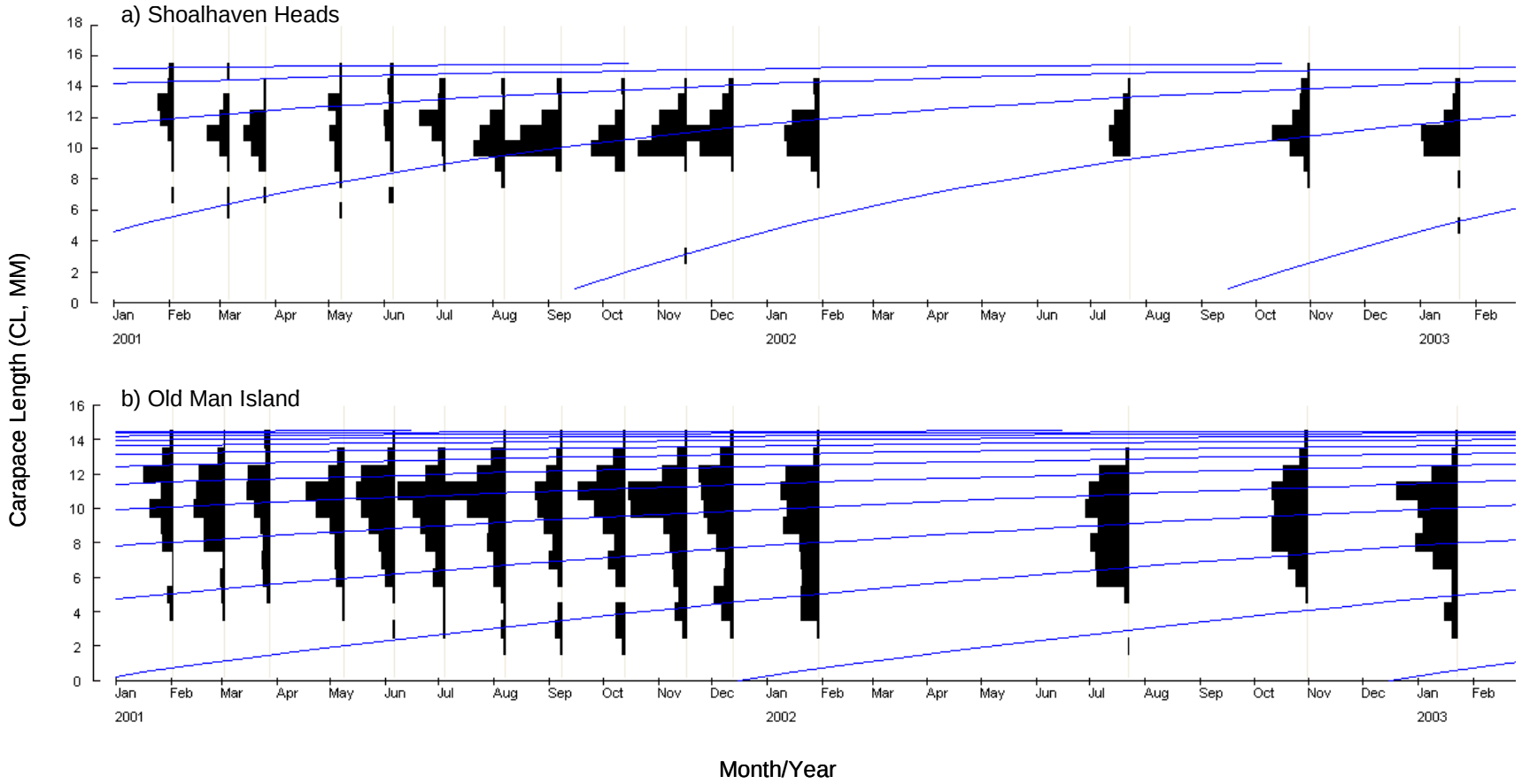


Figure 5.7. Length frequency distributions (CL, MM) and growth curves for *T. australiensis* at a) Shoalhaven Heads and b) Old Man Island in the Shoalhaven River between January 2001 and January 2003. See Table 5.9 for growth parameters.

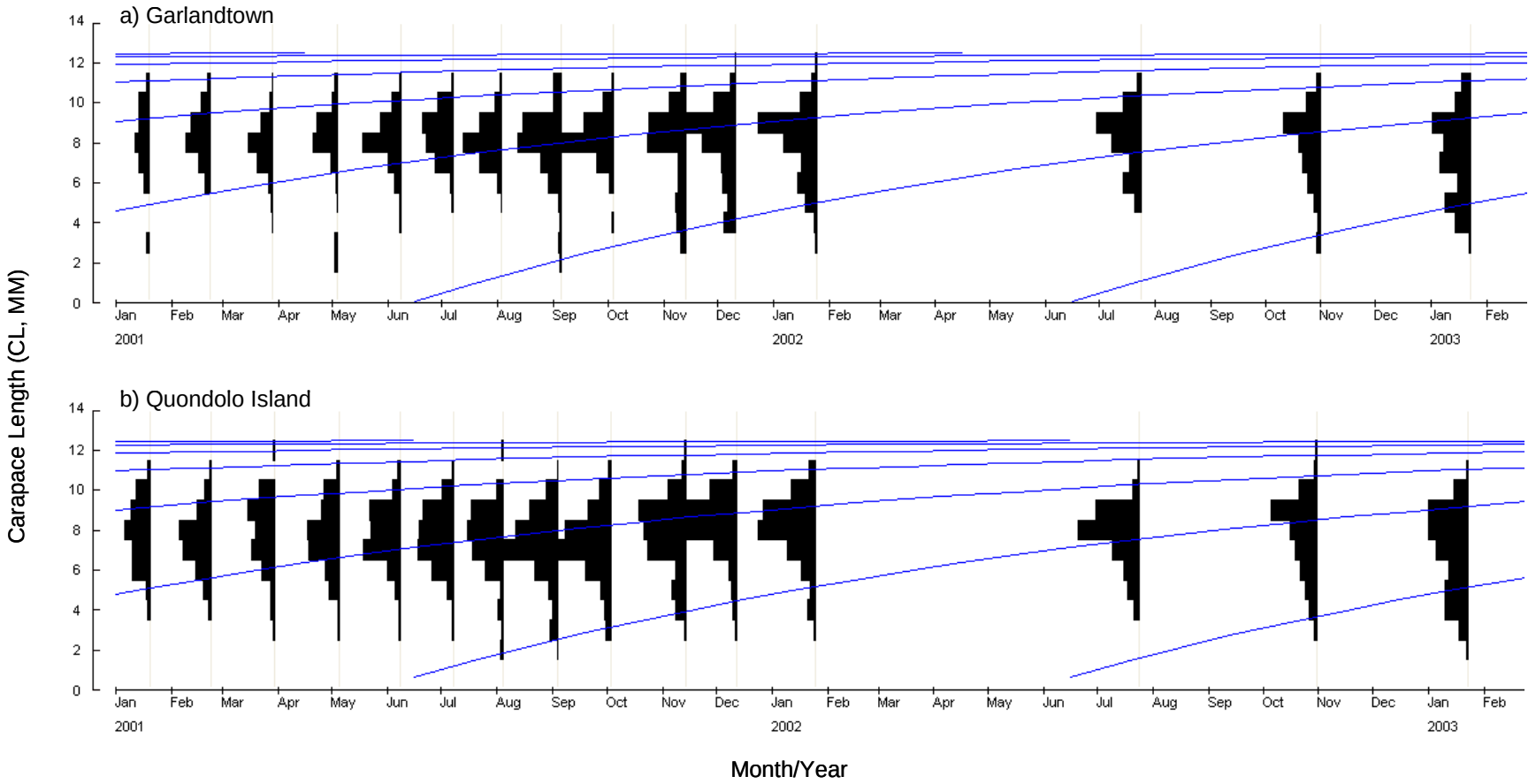


Figure 5.8. Length frequency distributions (CL, MM) and growth curves for *T. australiensis* at a) Garlandtown and b) Quondolo Island in the Moruya River between January 2001 and January 2003. See Table 5.9 for growth parameters.

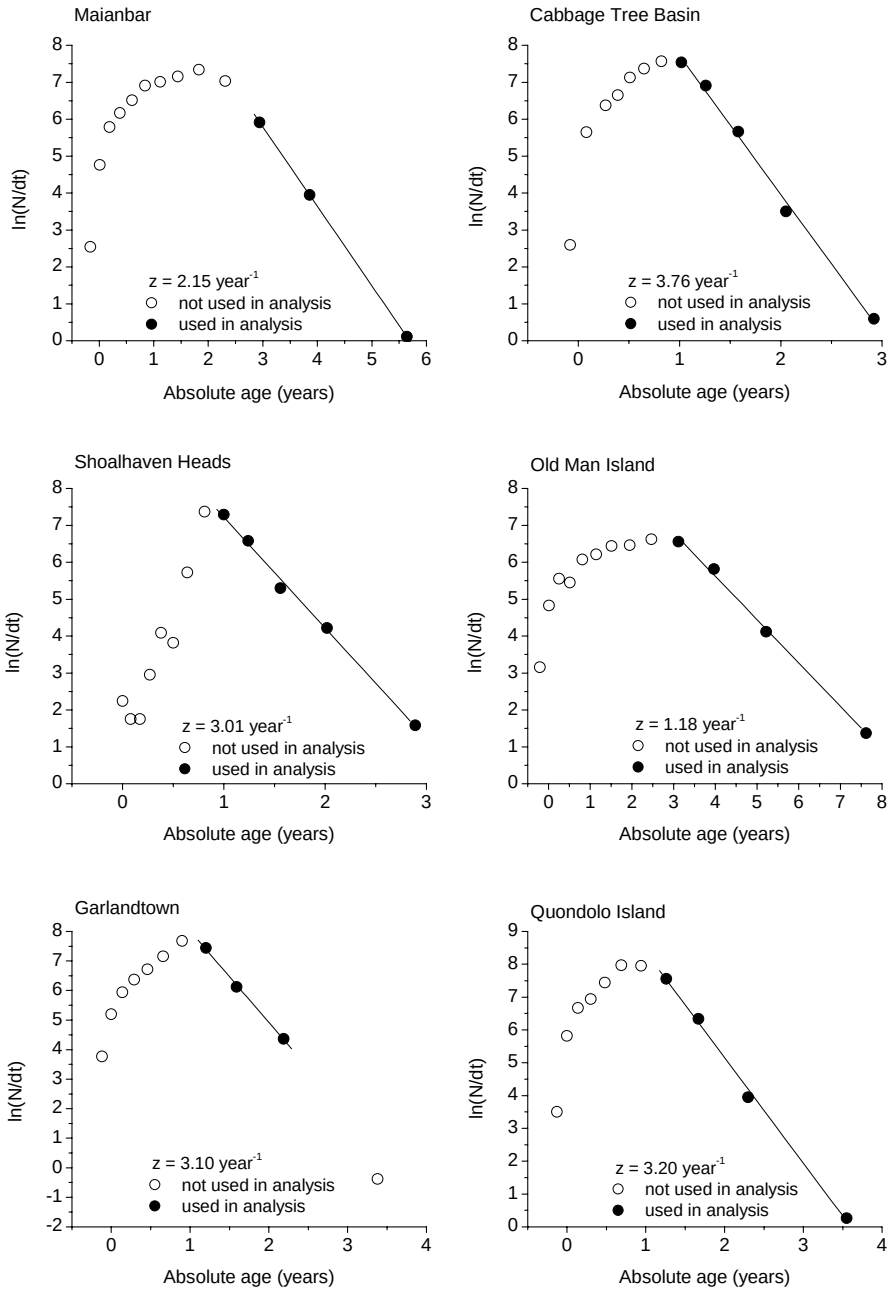


Figure 5.9. Length converted catch curves generated by FiSAT II estimating total mortality (*Z*) of *T. australiensis* at Maianbar, Cabbage Tree Basin, Shoalhaven Heads, Old Man Island, Garlandtown and Quondolo Island between January 2001 and January 2003.

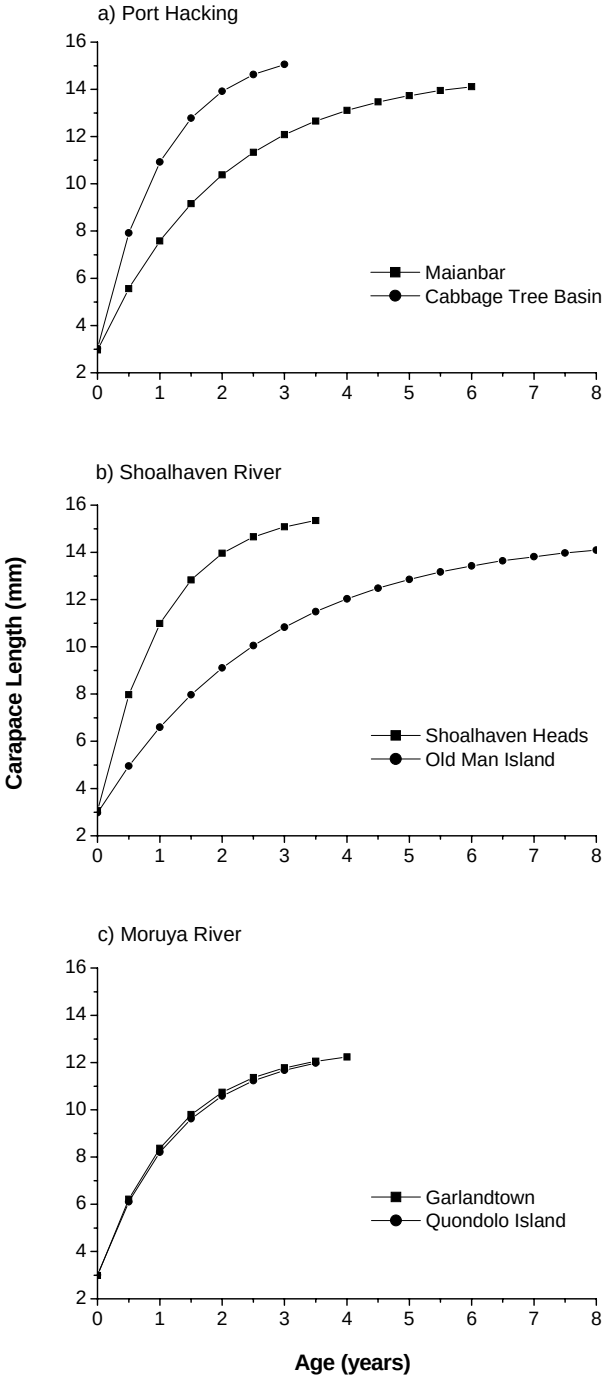


Figure 5.10. Von Bertalanffy growth curves ($L_t = L_\infty[1\text{-}\exp(1\text{-}k(t\text{-}t_0))]$) for *T. australiensis* at Maianbar and Cabbage Tree Basin in Port Hacking (a), Shoalhaven Heads and Old Man Island in the Shoalhaven River (b) and Garlandtown and Quondolo Island in the Moruya River. Asymptotic length (L_∞) and k were estimated using ELEFAN. Theoretical age at length zero (t_0) is not estimated by ELEFAN I and was therefore computed using the equation of Lopez Veiga (1979): $t_0 = (1\text{-}k)\ \ln\ (CL_\infty\text{-}CL_h/\ CL_\infty)$ (see text). Growth parameters are summarised in Table 5.9.

Table 5.10. Summary of previous studies of thalassinid ghost shrimp that have estimated parameters of the von Bertalanffy growth function, including k and L_∞.(CL, mm) using length frequency analysis for males (M) and females (F) or males and females combined (M+F). Phi values (φ') indicate growth performance index (Pauly and Munro, 1984). Software package shown where applicable.

Species	**Study area**	**Software**	***k***		***L*$_\infty$ (CL, mm)**		***φ'***		**Reference**
			M	F	M	F	M	F	
Sergio mirim	Cassino Beach, Brazil	ELEFAN	0.71	0.71	29.13	30.13	2.79	2.84	Pezzuto (1998)
Upogebia pusilla	Grado, Adriatic Sea	ELEFAN	0.5	0.5	25.2	21	2.50	2.32	Dworschak (1988)
Upogebia pusilla	Evros Delta, Greece	-	0.715	1.161	24	20	2.61	2.66	Kevrekdis *et al*., (1997)
Upogebia africana	Swartkops estuary, South Africa	-	0.699 (M +F)		24.40 (M +F)		2.62 (M + F)		Hanekom and Baird (1992)
Callichirus major	Atami beach, Brazil	ELEFAN	0.9	0.8	15	16	0.19	2.31	Souza *et al.,* (1998)

5.4 Discussion

Estimates of female size at maturity using REGRANS did not compare well with the smallest ovigerous individual in each population (Table 5.8). Although such comparisons are often made to validate size at maturity estimates from relative growth analyses (Felder and Lovett, 1989; Rowden and Jones, 1994; Dumbauld *et al.*, 1996; Berkenbusch and Rowden, 1998), they may lead to erroneous conclusions. For example, REGRANS estimates maturity based on the occurrence of a critical moult, often considered to be a puberty moult (Hartnoll, 1982) and the latter (i.e., appearance of ovigerous females) on reproductive condition. According to Hartnoll (1982), the puberty moult in decapods does not necessarily coincide with gonad maturation and reproductive development and mating may occur prior to or after this moult. Felder and Lovett (1989) used this argument to account for ovigerous females of *Callianassa louisianensis* being smaller than the calculated size at maturity using transition points. A similar trend has also been observed for a number of other thalassinids (Rowden and Jones, 1994; Dumbauld *et al.*, 1996; Berkenbusch and Rowden, 1998).

In the present research, the minimum sizes of ovigerous females were also smaller than the critical moults suggested by REGRANS (Table 5.8). However, the magnitude of difference between sizes estimated by each method was certainly greater than in previous investigations. Nevertheless, the transition points determined by REGRANS compared more favourably with the mean size of ovigerous females (perhaps a more logical comparison), despite being generally smaller (Table 5.8). This may indicate a precopulatory moult, as suggested by Hailstone and Stephenson (1961).

Male size at maturity, as calculated by REGRANS, was smaller than for females across all sites. Similar results have been reported for *T. australiensis* in Moreton Bay (Hailstone and Stephenson, 1961) and for other burrowing shrimp (Rowden and Jones, 1994; Dumbauld *et al.*, 1996). Few studies have attempted to account for such differences or explain the broader significance. Hailstone and Stephenson (1961) found that males of *T. australiensis* moulted approximately one month earlier than females and suggested that this may occur in order for hardened males to copulate with soft females. However, this small time difference may not account for the large differences in size at maturity between males and females estimated by REGRANS in the present study. As mentioned earlier, the use of relative growth parameters to estimate maturity may simply indicate separate growth phases, which could have little bearing on reproductive condition (Hartnoll, 1982). Despite appearing to undergo a puberty moult before females (CL v ChH, Tables 5.1 - 5.5), males may delay gonad development until some time after this moult.

A considerable body of anecdotal evidence suggests that the enlarged chela of male shrimp may be used in aggressive interactions with other males in competition for females or space (Hailstone, 1962; Tunberg, 1986; Rowden and Jones, 1994; Labadie and Palmer, 1996). Therefore, maturation of the testes may be deferred until chelae have reached a size large enough to allow individuals to be competitive in agonistic encounters with larger male shrimp. Certainly, future studies could consider estimating male size at maturity based on reproductive condition of testes (see Nurse, 1980), in addition to analyses of relative growth parameters.

Geographic differences were evident in the sizes at maturity estimated by REGRANS for both males and females, with individuals from southern estuaries maturing at smaller sizes than individuals from northern sites (Table 5.8). Patterns of maturity determined from REGRANS for females were not as strong as those determined from analyses of ovigerous females (see Chapter 4; Fig. 5.5, Table 5.8 in this chapter). Nonetheless, the pattern of decreased size with increased latitude for males appears distinct (Fig. 5.5, Table 5.8). Temperature and food availability are perhaps the most important external factors affecting crustacean growth (Kinne, 1970; Hartnoll, 2001). As discussed in relation to ovigerous females in Chapter 4, the observed patterns do not conform to the well known relationship between increasing latitude (and decreasing temperatures) and increased body size and size at maturity for other marine invertebrates (Kinne, 1970; Hastings, 1981; Jones and Simons, 1983; Levinton and Monahan, 1983). For example, Hartnoll (2001) suggests that although a decrease in temperature can result in decreased growth rates, it may ultimately result in larger individuals and an increased time period in reaching particular life-cycle stages. Consequently, the smaller sizes at maturity of individuals at the southern (colder) sites may not be explained by lower temperatures in this region alone. Higher population densities at these sites (see Chapter 3) may result in a reduction of food, acting to prolong the intermoult period, reduce moult increment (Hartnoll, 2001) and decrease size at maturity. As suggested in Chapter 4 of this thesis, further research is needed to examine the complex interactions between environmental factors, population densities and food availability on patterns of maturity observed in the present study.

An enlarged sexually dimorphic primary chela is a common feature of male thalassinid shrimp (Biffar, 1971; Poore and Griffin, 1979; Manning and Felder, 1991; Poore, 1994). Apparently there is no predisposition to left or right handedness of enlarged chelae within the family (Dworschak, 1988; Dworschak and Pervesler, 1988; Felder and Lovett, 1989; Rowden and Jones, 1994; Labadie and Palmer, 1996; Berkenbusch and Rowden, 1998; Dworschak, 1998), a trend which is also supported for *T. australiensis* in the present research (Table 5.7). The general pattern of positive, allometric growth of the primary chela for both sexes of shrimp up until maturity was also supported in the present research (see Hailstone and Stephenson, 1961; Devine, 1966; Dworschak, 1988; Felder and Lovett, 1989; Rowden and Jones, 1994; Dumbauld *et al.*, 1996; Dworschak, 1998). Following maturity, growth became increasingly allometric for males and negatively allometric for females (Fig. 5.2, Tables 5.1-5.6), resulting in different sized and shaped chelae (Fig. 5.3, Plate 1.1). Some authors have concluded that the absence of an enlarged chela in female thalassinid shrimp is due to investment of energy in egg production (Tucker, 1930). This can be measured as an increase in weight or total length without a corresponding increase in carapace length (Felder and Lovett, 1989), which occurred for *T. australiensis* in the present study (see Fig. 5.4 and Tables 5.1-5.5). However, Felder and Lovett (1989) argue that development of an enlarged primary chela in males may serve a specific behavioural function, given differences in shape and the fact that total weight of large males can exceed that of ovigerous females.

Morphometric analyses on claw size and shape variation of a closely related species, *Neotrypaea californiensis*, support the hypothesis that the primary chela

is used to grapple with other males during territorial agonistic interactions or mating (Labadie and Palmer, 1996). It was suggested that primary chelae of *T. australiensis* may serve a similar function, as it is the only thalassinid that has a deeper propodal notch than *N. californiensis*. According to Labadie and Palmer (1996), a deep propodal notch is indicative of a grappling function, rather than crushing. Grappling behaviour has been observed in forced encounters of *T. australiensis* in aquaria (Hailstone, 1962). Large males attempted to break off the primary chela of the other, with the victor ramming the loser out of the artificial burrow (a glass tube), with the losers own chela. However, when adult females or juveniles were placed with the male, they were tolerated after some preliminary "sparring". It was also noted that when two adult females were placed together, preliminary fighting was not sustained, with animals avoiding each other afterwards. Labadie and Palmer (1996) suggested that the gape of large *N. californiensis* may be too large to grasp the smaller claws of females or juveniles. This may also explain the above observations of Hailstone (1962) for *T. australiensis*. However, Labadie and Palmer (1996) also point out that such behaviour may be artefacts of forced unnatural encounters outside burrows, as experiments conducted in laboratory fossoria often yield no information on agonistic encounters and their significance for mating systems, due to the difficultly observing animals within burrows.

The present research is the first to estimate parameters of the von Bertalanffy growth model for *T. australiensis* using ELEFAN. Similar analyses have been conducted for only a few thalassinids (Table 5.10), which includes just a single callianassid. There were no consistent geographic trends in growth parameters,

except for smaller asymptotic lengths (L_∞) at sites within the Moruya River, which reflects the smaller size of animals within this estuary. With the exception of Maianbar and Old Man Island, the *k* values reported here for *T. australiensis* are among some of the highest for the taxa (Table 5.10). In comparison, asymptotic lengths (L_∞) and growth performance indices (φ') were low. Munro and Pauly (1983) suggested that the reliability of estimated growth parameters (L_∞ and *k*) may be evaluated through comparisons of phi (φ') within the same family, which should be similar and normally distributed. Pezzuto (1998) suggested that higher values of phi for *S. mirim* (a callianassid), may indicate differences in growth performance between the Callianassidae and Thalassinidea. However, the present research suggests little difference between families, as estimates of phi for *T. australiensis* are the lowest reported for any thalassinid or callianassid. Unlike Pezzuto (1998), the values of phi in the present research covered a wide range, suggesting either inaccuracy of estimated values, or differences in growth performance between sites. Further research is suggested to determine if *S. mirim* and *T. australiensis* represent upper and lower limits respectively for the Callianassidae.

Longevity of *T. australiensis* ranged between 3 and 4 years across most sites, which is greater than the 2 to 3 years estimated by Hailstone and Stephenson (1961). Although estimates of 6 to 8 years were obtained for Maianbar and Old Man Island, these results are likely to be an artefact of ELEFAN analyses. The shorter life-span reported by for populations of *T. australiensis* at Moreton Bay in Queensland (Hailstone and Stephenson, 1961), may reflect higher growth rates in this region due to higher temperatures (after Kinne, 1970; Hartnoll, 2001). It is

important to note that the life-span of *T. australiensis* in Moreton Bay was determined graphically from interpretations of length frequency histograms (Hailstone and Stephenson, 1961), which may equally account for differences between the results based on parameters from ELEFAN in the present study. Previous studies in Moreton Bay also showed that individuals reached approximately 9.5 mm in length after one year of growth (Hailstone and Stephenson, 1961). Similar sizes were obtained for Cabbage Tree Basin and Shoalhaven Heads after the same time period in the present study. However, growth rates were slower for other sites, which may reflect local environmental factors and/or population dynamics, or perhaps even the inaccuracy of the ELEFAN procedure. High growth rates and short life-spans are common for other burrowing ghost shrimp (Table 5.10) (Devine, 1966; Forbes, 1977a; Dworschak, 1988; Dumbauld *et al.*, 1996; Kevrekidis *et al.*, 1997; Tamaki *et al.*, 1997). For example, only one species of thalassinid is reported to live longer than 5 years (e.g., *Calocaris macandreae*, 10 years; Buchanan, 1963). Based on estimates of sexual maturity from ovigerous females and analyses of relative growth (REGRANS) in the present study, *T. australiensis* appears to begin to reproduce about 12 months after settlement as post-larvae (Table 5.8, Fig. 5.10). This result is similar to that of previous studies (Hailstone and Stephenson, 1961), and indeed studies of other burrowing shrimp (Rowden and Jones, 1994; Tamaki *et al.*, 1997; Berkenbusch and Rowden, 1998).

Patterns of fishing mortality (F) and exploitation ratio (E) (Table 5.9) in the present research were not consistent with general observations of recreational harvesting activities. For example, Cabbage Tree Basin had the highest estimates

of fishing mortality and exploitation (Table 5.9), although the author only encountered a single harvester at this location during the study period. Given that the area of sandflats at Cabbage Tree Basin were less extensive than at popular harvesting locations such as Maianbar, the high fishing mortality at this site may in fact represent sampling activities of the present study. Hailstone and Stephenson (1961) terminated sampling at a site in Moreton Bay because these activities were depleting standing stocks of *T. australiensis*. Note however that in the present study, abundances of *T. australiensis* increased at all sites throughout the study period (see Chapter 3). The low fishing mortality and exploitation ratio at Old Man Island was expected, since no parties were ever observed harvesting at this location. For the most intensively harvested sites such as Maianbar and Garlandtown (see also Chapter 5), exploitation ratios were almost identical and were under $E_{opt} = 0.50$. In fact, values of E were under or approximately equal to 0.50 for all sites (Table 5.9), which suggests that populations are currently under-exploited or at least below optimal harvesting rates. It must be stressed, however, that estimates of mortalities and exploitation ratios in the present study are preliminary in nature and caution should be exercised in their interpretation, since they were derived from outputs of ELEFAN, which may prove unreliable.

The reliability of the ELEFAN procedure has been assessed using simulated length frequency distributions from known growth parameters for some fish and invertebrates (Hampton and Majkowski, 1987; Rosenberg and Beddington, 1987; Jackson *et al*., 2000). Some results of these studies indeed challenge the validity of the procedure. For example, ELEFAN was shown to be unsuitable for application to organisms that grow exponentially, as it assumes a wrong model of

asymptotic von Bertalanffy growth (Jackson *et al.*, 2000). Furthermore, for fast growing species with individual plasticity and multiple cohorts, similar sized animals may have different ages, making detection of modes in length frequency data difficult (Jackson *et al.*, 2000). Modal progression of cohorts was certainly evident for *T. australiensis* in the present study (Figs. 5.6 - 5.8). Whilst ELEFAN appeared to fit data quite well for some sites, growth curves still often missed modes, and multiple curves were drawn through single cohorts or non-existing data. This situation seems commonplace in a number of other studies that have employed ELEFAN on growth of fishes (Perez-Espana *et al.*, 1998; Ofori-Danson *et al.*, 2001; Mateus and Estupinan, 2002; Ozbilgin *et al.*, 2004) and invertebrates (Oh *et al.*, 1999), and may explain the apparent anomalies for data from Maianbar and Old Man Island in the present research.

Alternative explanations for poorly fitting data and missing size classes for some months may include the high mobility of *T. australiensis* as hypothesized in Chapter 3 and Appendix 1. Improved fitting of data and better representation of some length classes may also be obtained from larger sample sizes. Although, sample sizes in the present research were greater than for many previous investigations of other species of burrowing shrimp. Hanekom and Baird (1992) demonstrated clearer modal progression from length data containing > 400 individuals of *U. africana* from single sites in the Swartkops Estuary in South Africa. The primary reason why growth was not described separately for each sex in the present study was due to the female-biased sex ratios (see Chapter 4), which resulted in small sample sizes for males. Future studies should attempt to increase sample sizes to allow for separate analyses of growth for each sex by increasing

replication of plots within sandflat sites, which is the spatial scale where most variation occurred in the present research (see Chapter 3).

Estimates of seasonal oscillation (C) and winter point (WP) were not calculated by ELEFAN for *T. australiensis* in the present study, due to an apparent software error within the FiSAT package (F. Gayanillo, pers. comm). It was suggested by D. Pauly (pers. comm) that these parameters may be estimated using tagging experiments. Although the use of internal tags appears promising for *T. australiensis* (Appendix 1), the difficulty in keeping animals alive for extended periods makes good estimations of C and WP difficult at this stage. Nevertheless, estimates of these parameters may also provide better fits of length frequency data in future investigations.

The present research has described and compared relative and absolute growth parameters for *T. australiensis* over wide spatial and temporal scales, from a quantitative hierarchical sampling program in south-eastern Australia. Sizes at maturity, determined from analyses of relative growth parameters appeared to be related to latitude, with populations in southern estuaries maturing at smaller sizes than those further north. The enlarged primary chela possessed by male *T. australiensis* resulted from differences in allometric growth between sexes following maturity. Males also matured at smaller sizes than females.

Despite questions of reliability, appropriateness, and the need to interpret results with caution (Hilborn and Walters, 1992; Jackson *et al.*, 2000; Hartnoll, 2001), length frequency analyses using ELEFAN currently provide “best estimates” of

growth for *T. australiensis* and other thalassinids, given the difficulties in ageing shrimp using traditional tagging methods or examination of hard parts (see above). Comparisons with other more objective electronic length frequency packages such as MIX (Macdonald and Pitcher, 1979; Macdonald and Green, 1988) and MULTIFAN (Fournier *et al.*, 1990) are beyond the scope of this thesis but may be considered in a future publication.

Management implications resulting from the present study are discussed in Chapter 7, together with a discussion of the life-history of *T. australiensis* in south-eastern Australia and directions for future research.

Chapter 6

Recreational harvesting of *Trypaea australiensis* in south-eastern Australia

6.1. Introduction

Harvesting of shoreline biota from marine environments is a popular recreational activity in many developed countries, given the large numbers of people that live within, or in close proximity to the coastal zone. Motives for harvesting are varied, with individuals collecting a range of plants, and invertebrate animals including crustaceans, molluscs, polychaetes, ascidians and echiurans for food, bait, and home aquaria. Harvesting may also be secondary to other recreational pursuits, with collecting being of an opportunistic nature for curios and keepsakes. Certainly, recreational harvesting of food and bait organisms forms large unorganised fisheries, with catches that may be comparable to or greater than subsistence and commercial sectors (McLachlan *et al.*, 1996).

The effects of subsistence and commercial harvesting on populations of marine invertebrates, such as reductions in mean size and density of target species has been well documented (Moreno *et al.*, 1984; Castilla and Duran, 1985; Siegfried *et al.*, 1985; Hockey and Bosman, 1986; Moreno *et al.*, 1986; Olivia and Castilla, 1986; Duran *et al.*, 1987; Castilla and Bustamante, 1989; Duran and Castilla, 1989; Fairweather, 1990a). Some studies have also investigated the indirect effects of such activities on local ecology (e.g., Moreno *et al.*, 1984; Castilla and Duran, 1985; Moreno *et al.*, 1986; Duran and Castilla, 1989; Godoy and Moreno, 1989; Underwood, 1993a; Dye, 1995). In comparison, relatively few studies have considered the impacts of recreational collecting either on target organisms

(Jackson and James, 1979; Catterall and Poiner, 1987; Keough *et al.*, 1993; Wynberg and Branch, 1994), or at an ecosystem level (McLusky *et al.*, 1983; Wynberg and Branch, 1997; Sharpe and Keough, 1998). This is perhaps due to a common perception that the individual impacts of recreational fishers are relatively benign (Kearney, 1999, 2001; McPhee *et al.*, 2002).

The broader ecological implications of commercial fishing activities on non-target species and habitats and the general inadequacy of traditional "single-species" approaches to fisheries management have been increasingly addressed in recent years (Botsford, 1997; Hanna, 1999; Pitcher, 2001). In many cases this has resulted in changes to, or cessation of, some deleterious fishing practices, including investigations of gear modifications which may reduce by-catch (e.g., Andrew and Pepperell, 1992; Poiner and Harris, 1996; Broadhurst *et al.*, 1999; Gray *et al.*, 2000; Kennelly and Gray, 2000; Broadhurst *et al.*, 2002; Fonteyne and Polet, 2002). In contrast, much of the research on recreational fishing, particularly in Australia, is still concerned with assessing catch and effort of key species of finfish, often to the exclusion of many bait organisms (Henry, 1984; West and Gordon, 1994; Kearney, 1995; Steffe *et al.*, 1996; McPhee *et al.*, 2002; Henry and Lyle, 2003). While there is a growing realisation that the recreational catch of certain species of finfish exceeds that of the commercial sector (McGlennon, 1992; Pollock *et al.*, 1994; West and Gordon, 1994; Ferrell and Sumpton, 1998), and that the cumulative impacts of recreational fishing may be large (McPhee *et al.*, 2002), characteristics of the catch and effort of many important invertebrate bait fisheries remains relatively unknown, particularly in NSW. Consequently, conservation of these species has frequently been conducted in an *ad-hoc* fashion,

relying largely on anecdotal evidence as the "best available information" (after Smith and Pollard, 1996), on which to support management decisions, or lack thereof.

Some studies suggest that the recreational harvest of intertidal bait organisms may be significant, particularly from rocky shores (Underwood and Kennelly, 1990; Fairweather, 1991; Kingsford *et al.*, 1991; Underwood, 1993a). However, bag and size limits, as well as marine reserves (e.g., marine protected areas and intertidal protected areas), now protect rocky shore biodiversity in a number of areas in NSW (Anon, 2004d). Despite the potential magnitude of harvests from other habitats, including intertidal sandflats (Murray-Jones and Steffe, 2000), no regular monitoring of recreational catches of bait organisms is undertaken in NSW, and soft-sediment habitats are under-represented in marine reserves (Anon, 2004d). For some popular bait species such as the ghost shrimp, *T. australiensis*, there are no restrictions on catch numbers or weights currently in effect.

A recent survey of recreational fishing in Australia indicated that *T. australiensis* was the second most harvested species by numbers in NSW, with an estimated 3,033,392 animals harvested per annum (Henry and Lyle, 2003). Nationally, it was the most harvested species by the recreational sector, with an estimated 20,082,936 animals taken by anglers for bait. Given that these estimates are derived from off-site interviews and angler surveys, there would be large associated errors. For example, anglers may misreport catch and effort estimates in these surveys through recall and/or prestige bias, and catches cannot be directly examined by the interviewer (Pollock *et al.*, 1994). In fact, it has been suggested

that telephone based surveys should not be undertaken for abundant species that are frequently harvested (Pollock *et al.*, 1994). By comparison to the figures quoted above for NSW, on-site studies of a closely related bait species from South Africa, *Callianassa kraussi*, found that recreational harvesters removed over 1,222,500 shrimp per annum from a single lagoon (Wynberg and Branch, 1991). Also in South Africa, bait harvesters collected an estimated 1,800,000 individuals of the mud shrimp *Upogebia africana* from the Knysna estuary per annum (Hodgson *et al.*, 2000b). Similar data from on-site creel surveys do not exist for *T. australiensis* at individual sites in NSW. However, McPhee and Skilleter (2002b) estimated that 3,900 individuals of *T. australiensis* were harvested from two locations in Moreton Bay (Queensland), during a one-week fishing tournament. In addition to the restricted temporal scale, this study was primarily limited to tournament participants, who are perhaps more skilled than many other anglers, and are likely to use less bait animals to catch a greater number of fish. These participants were also boat-based anglers and previous studies have shown differences between the harvesting characteristics of boat and shore based anglers (West and Gordon, 1994). Many popular harvesting locations for *T. australiensis* in NSW are accessible by foot and have car parks in close proximity. Therefore, higher numbers of shore-based anglers are expected to dominate these sites, and have different needs to boat-based harvesters, which use their bait immediately within the waterway.

The lack of a current management strategy for *T. australiensis* in NSW highlights the difficulties in prescribing traditional fisheries strategies to this species, a situation complicated by a lack of data. Conservation measures have been

implemented for other invertebrates in NSW based on the precautionary approach and anecdotal evidence (Smith and Pollard, 1996), but not for *T. australiensis*. Unfortunately, anecdotal information on the status of *T. australiensis* in NSW varies between locations and is often contradictory, further explaining the absence of conservation measures for this species. Clearly, the current situation of almost unrestricted open access is undesirable, particularly since a greater share of fisheries resources are being shifted from the commercial to recreational sector. Combined with sustained population growth in urban centres, this may ultimately see the demand for bait species increase.

The need to assess impacts of recreational fishing on aquatic biodiversity has been highlighted under Australia's local and international obligations to ecosystem based approaches to management, outlined in the ESD Fisheries Working Group (Anon, 1992) and Australia's Ocean Policy (Anon, 1998) (see McPhee *et al.*, 2002). Whilst many researchers advocate protection of key stocks of fish and invertebrates within reserves as part of an ecosystem approach to conservation, populations outside reserves still require management based on sustainable strategies. Some authors argue that restrictions such as bag limits generally do little to protect fish stocks, as they are set too high to allow sustained conservation (Underwood, 1993a; Ferrell and Sumpton, 1998). However, bag limits may be set effectively when information on catch, effort, population size and the biology and ecology of an organism is known (Attwood and Bennett, 1995).

Estimates of the total harvest of *T. australiensis* for particular estuaries, zones and states, like those obtained from the National Recreational and Indigenous Fishing Survey (Henry and Lyle, 2003), may be useful for setting overall priorities, but are of less use for prescribing management strategies such as bag limits, which often require more detailed data such as harvest per person at individual locations (Underwood, 1993a). For *T. australiensis*, such catch and effort data for individual fishers in NSW waters does not exist.

Information on the population biology and ecology of *T. australiensis* has been provided in previous chapters of this thesis and should assist in the management of the species. The present chapter provides information on the extent and intensity of the recreational catch and effort of *T. australiensis* at selected sites in south-eastern Australia, an important component of an ecosystem based approach to conservation and management of the species. The specific aims of this chapter were to: (1) estimate and compare Catch Per Unit Effort (CPUE), effort and mean daily harvest of *T. australiensis* during low-tide periods, between three popular harvesting sites in south-eastern NSW in spring and summer; (2) collect information on the characteristics of harvesting including fisher demographics, party size, harvesting frequency and retention of small individuals and ovigerous females; (3) provide estimates of the total catch of *T. australiensis* at each site over the study period; (4) compare results (where possible) to the National Recreational and Indigenous Fishing Survey (Henry and Lyle, 2003) and discuss the utility of telephone based surveys for estimating catches of this species.

6.2. Materials and methods

6.2.1 Sampling design

The activities of recreational bait-harvesters were examined at selected sites along a 300 km stretch of the coast of south-eastern NSW between September 2002 and February 2003. Access point creel surveys were conduced at one site in each of the three estuaries sampled in the main study and included; Maianbar (Port Hacking), Shoalhaven Heads (Shoalhaven River) and Garlandtown (Moruya River) (see maps in Fig. 1.1 and Figs. 3.1 - 3.3, in previous chapters of this thesis). These sites were selected because they represented areas that are easily accessible (i.e., they do not require a boat or long walk) and represent popular harvesting locations for *T. australiensis* in the region. In addition, each site had one main access point via a car park on the shore. Given that only one site was sampled from each estuary, results can only be interpreted for the particular site in question and cannot be extrapolated to entire estuaries.

As an intertidal animal, *T. australiensis* is harvested primarily during low-tide periods. Therefore, the creel survey was designed around low-tide intervals. The study period was divided into seasonal strata (spring: September-November; summer: December-February) and three replicate days were randomly sampled from each. Summer was further divided into day-type strata (i.e., weekend/public holiday/school holiday and weekdays (term time). The extended school holiday/Christmas/New Year period during summer provided more replicates of the weekend/public holiday/school holiday day-type that would normally exist in other seasons. Therefore, the lower number of weekend/public holiday/school

holiday days in spring, combined with the restrictive low-tide time-frame in which surveys were conducted on each day (see below), meant there were insufficient replicates to enable stratification into day-type across all sites. Hence, only weekdays during term time were sampled in spring.

Creel surveys were conducted in daylight hours (9am to 6pm in spring and 9am to 7pm in summer) and included an entire low-tide period. Each survey commenced three hours before low-tide and ended three hours after. As a result, only low-tides occurring between 12pm and 3pm were included in the study for spring periods, and between 12pm and 4pm for summer. These times ensured that harvesting activities were surveyed for an entire low-tide period as it was assumed that in between these hours, tide, rather than time of day, affects numbers of harvesters.

On each sampling occasion, the creel clerk arrived at a site three hours before low-tide and set up a station at the access point, in a position that allowed a view of the entire sandflat area with binoculars. As harvesters arrived at the site the number of people in each harvesting "party" and the number of stainless steel yabby pump devices, which are used to harvest *T. australiensis* from their burrows, were counted. While a harvesting party may consist of a number of people, not all members actively harvested. For example, some may assist by picking up shrimp which have been expelled from the yabby pump, whilst others simply observe. Some members of a party may also take turns pumping. In the present study, the term "observer" is used to define members of harvesting parties that are not actively pumping, rather than "helper", which was used in a previous study (McPhee and Skilleter, 2002b). The time at which harvesting commenced

and finished was recorded (not the times when a party arrived and departed the access point). For example, some parties often took a considerable amount of time to begin harvesting once they arrived at a sandflat, preferring to walk to certain areas, in some cases as far as 400 m from the access point. Also, parties often took a long time to leave the sandflat after harvesting, walking back from remote areas of the site to the access point. Simply recording the trip times (i.e., the times a party passed through the access point) would therefore bias estimates of catch rate. The sex of harvesting party members was recorded and ages estimated as youth (0 - 18 years), adult (18 - 55) and elderly (55 +).

As each harvesting party approached the access point to leave the sandflat after finishing bait-collecting activities, they were approached for an interview. Parties were asked if they would participate in the survey and presented with an information sheet. If consent was given, the primary harvester (i.e., the one that did most of the pumping) was identified and asked the following open-ended questions:

1. How long have you been harvesting?
2. How many did you catch?
3. How often do you harvest nippers? Which seasons? Why?
4. Do you throw back small nippers?
5. Do you throw back nippers carrying eggs?
6. Can I count your catch?

Although closed-ended questions are often more controlled and easier to interpret in angler surveys (Pollock *et al.*, 1994), the above questions were considered simplistic enough to summarize quantitatively. Closed-ended questions generally require *a-priori* knowledge of harvesting activities. However, the activities of bait harvesters in south-eastern NSW are generally unknown. The use of closed-ended questions may also be difficult in field situations, as the angler cannot see the response categories (compared with a mail-survey) and must rely on the interviewer, which may lead to confusion and inaccurate responses. Another important consideration was that closed-ended questions would result in a much longer interview, which may potentially irritate participants and result in higher numbers of anglers that are missed whilst a particular party is being interviewed.

Initially, it was intended to gather size frequency information on the recreational catch of *T. australiensis*. However, it became apparent that most anglers strongly objected to their catch being handled, citing the fragility of the animal as well as the potential time taken to measure a representative sample. The aggressive nature of the animals, combined with their enlarged chela and snapping movement of the abdomen, also made accurate field measurements extremely difficult. Therefore, size ranges of catches were assessed qualitatively by visual means. Similarly, many anglers declined to have their catches counted but allowed an estimate to be made without handling the catch. In instances where people declined to have their catch counted by any means, a visual estimate was still made. In some situations, anglers concealed their catches with lids and refused an interview. As expected, people at some sites accessed the sandflat by boat and did not pass through the car park based access points, and could not be interviewed. Nevertheless, their

harvesting activities were still observed and quantified. Interviews in the present study are of shore-based anglers only, which arrived and departed via the car park access points to each site. Where possible the results of the present study have been compared with unpublished data from the National Angler and Indigenous Fishing Survey (Henry and Lyle, 2003) conducted by telephone interviews and diaries (supplied by G. Henry, NSW Fisheries).

6.2.2. Statistical analyses

Differences in mean harvesting time between boat and shore-based harvesters were compared using separate *t*-tests for each site, due to absence and/or unequal numbers of boat and shore harvesters at some sites on certain occasions. Two-factor analysis of variance (ANOVA) was used to compare mean number of harvesting parties between sites and season/day-type; mean number of harvesters between incoming and outgoing tides and sites; mean Catch Per Unit Effort (CPUE) between sites and season/day-type; mean number of harvesting minutes (effort) between sites and season/day-type and; mean daily catch (catch) between sites and season/day-type. All factors in all analyses were considered fixed. Data were examined for normality and homogeneity of variances using Shapiro-Wilk and modified Levene's tests respectively and transformed to *log* (x+1) where necessary. Means comparisons were done using Student-Newman-Keuls (SNK) tests.

6.2.3 Catch and effort estimation methods

For each day (6-hour low-tide period), total catch was estimated as CPUE (number of *T. australiensis*/min, determined from angler interviews) multiplied by total effort (total number of harvesting minutes, determined from direct observations). Mean daily catch was then calculated for each day-type strata by summing daily totals and dividing by the number of sampling days. Total catch for each day-type strata was calculated by multiplying mean daily catch by the number of possible 6-hour low-tide periods (determined by summing all low-tide minutes, three hours before and three hours after low-tide, between 9am - 6pm in spring and 9am - 7pm in summer). Seasonal catches were calculated by summing day-type totals. Since weekends/holidays/public holidays were not sampled in spring, all days in this season were treated as weekdays and hence totals are considered a minimum for this period. Totals for the entire study period were then calculated by summing seasonal totals. Variances and standard errors were calculated according to Pollock *et al*. (1994).

6.3 Results

6.3.1 Creel survey

A total of 252 parties were observed collecting *T. australiensis* during the study period, with more people harvesting at Maianbar and Garlandtown compared to Shoalhaven Heads (Table 6.1). At the two former locations, most people entered sandflats via shore-based access points. In contrast, access via shore and boat at Shoalhaven Heads was approximately equal. The percentage of harvesting parties remaining on-site and fishing with their bait immediately was relatively consistent

between sites and quite low (7 - 13%). Approximately 60% or more of shore-based harvesting parties excluding on-site fishers were approached for an interview at each site, for a total of 97 interviews. The remaining parties either refused to participate, or left the site whilst other parties were being interviewed.

The majority of harvesting parties comprised either a solitary harvester and/or one or two observers (Fig. 6.1). Larger parties with up to as many as 10 people were observed but relatively uncommon. Harvesting party demographics were fairly consistent over all sites and compare well to estimates by NSW Fisheries for the entire state of NSW, with the majority of harvesters generally adults (18 - 55 years) and youths (0 - 18 years) (Table 6.2). NSW Fisheries reported a higher proportion of elderly (55+ years) harvesters than the present study. Although, approximately 7 to 8% of people in the present study, which were mainly boat-based harvesters, could not be aged even with binoculars, because of the distance from the creel clerk (in some cases 500 m) and wearing of hats and sunglasses.

Table 6.1. Summary of recreational harvesters observed at Maianbar, Shoalhaven Heads and Garlandtown during creel surveys between September 2002 and February 2003, showing number of parties observed, platform (boat or shore), percentage that fished immediately with their bait on-site and number of interviews conducted. Parties engaged in on-site fishing were not approached for an interview.

Site	No. of Parties	Platform		On-site Fishing	No. of interviews
		Boat	Shore		Shore-based (OSF excl.)
Maianbar	150	54 (36%)	96 (64%)	19 (13%)	50 (67%)
Shoalhaven Heads	27	13 (48%)	14 (52%)	2 (7%)	8 (67%)
Garlandtown	75	4 (5%)	71 (95%)	5 (7%)	39 (59%)

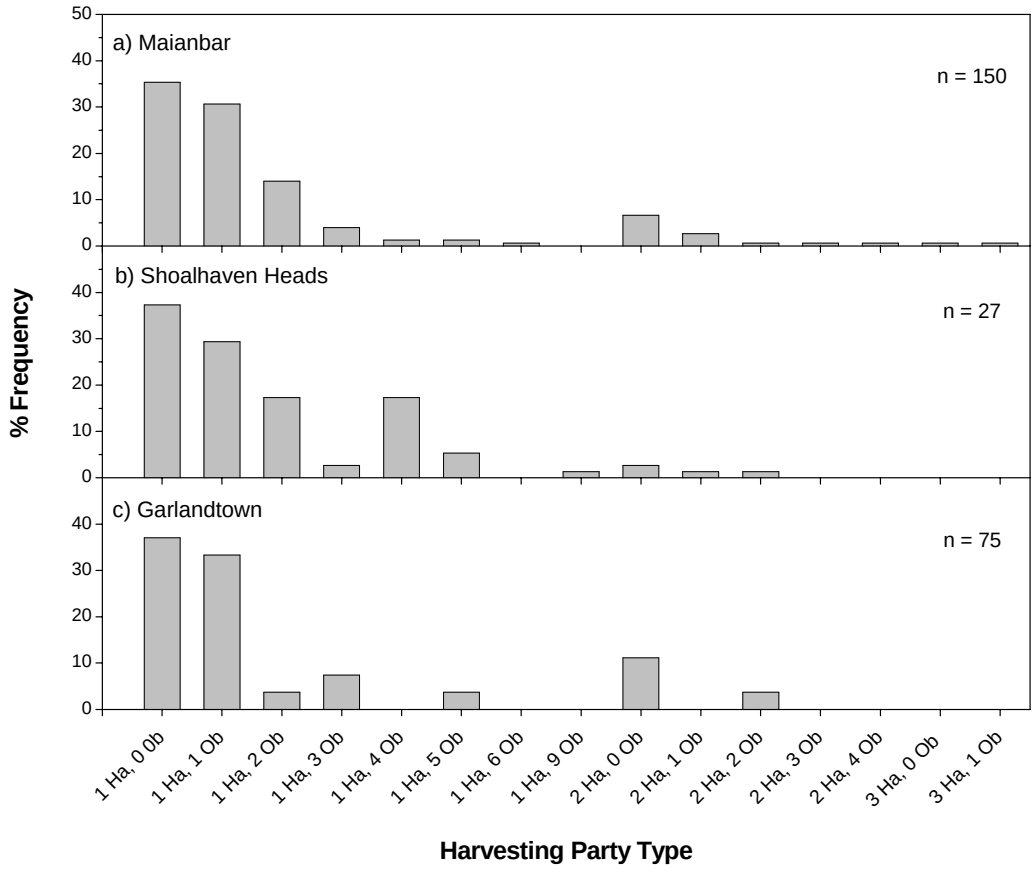


Figure 6.1. Frequency histograms showing the size and composition of harvesting parties collecting *T. australiensis* for bait at Maianbar, Shoalhaven Heads and Garlandtown, between September 2002 and February 2003. Ha = Harvester, Ob = Observer (see text for definitions).

Table 6.2. Summary of the demographics and sex ratio of harvesting parties collecting *T. australiensis* for bait at Maianbar, Shoalhaven Heads and Garlandtown between September 2002 and February 2003. Data for NSW supplied by G. Henry (NSW Fisheries).

	Age Group				Sex		
Site	Youth (0-18)	Adult (18-55)	Elderly (55+)	Unknown	Male	Female	Unknown
Maianbar	28%	55%	10%	7%	86%	13%	1%
Shoalhaven Heads	28%	49%	15%	8%	88%	12%	0%
Garlandtown	30%	51%	19%	0%	72%	24%	4%
NSW	21%	52%	27%	0%	76%	24%	0%

There were no significant differences in the mean time spent harvesting by bait harvesters at each site (one-way ANOVA, $F = 2.17$, $P > 0.05$). The majority of people spent 31 - 45 minutes harvesting at Maianbar and Shoalhaven Heads, compared with 16 - 30 minutes at Garlandtown (Fig. 6.2). Small percentages of parties harvested longer than 90 minutes at Maianbar and Garlandtown, whilst at Shoalhaven Heads, no party harvested longer than 75 minutes. Boat-based harvesters spent significantly less time harvesting than shore-based anglers ($P < 0.05$, *t*-tests) at all sites except Shoalhaven Heads, even though a similar trend was evident (Fig. 6.3).

ANOVA revealed significant differences between sites and seasons/day-type for the mean number of harvesting parties (Fig. 6.4, Table 6.3). Significantly more parties harvested at Maianbar compared to Shoalhaven Heads and Garlandtown (SNK tests). More parties also harvested at Garlandtown compared to Shoalhaven Heads (SNK tests). Although the mean number of parties was higher on summer weekdays across all sites, differences between seasons/day-type were only significant for Maianbar. There were no significant differences between spring weekdays and weekends at any site. Despite a trend of more parties commencing harvesting during outgoing tides across all sites (Fig. 6.5), differences between incoming and outgoing tides were not significant (Table 6.4).

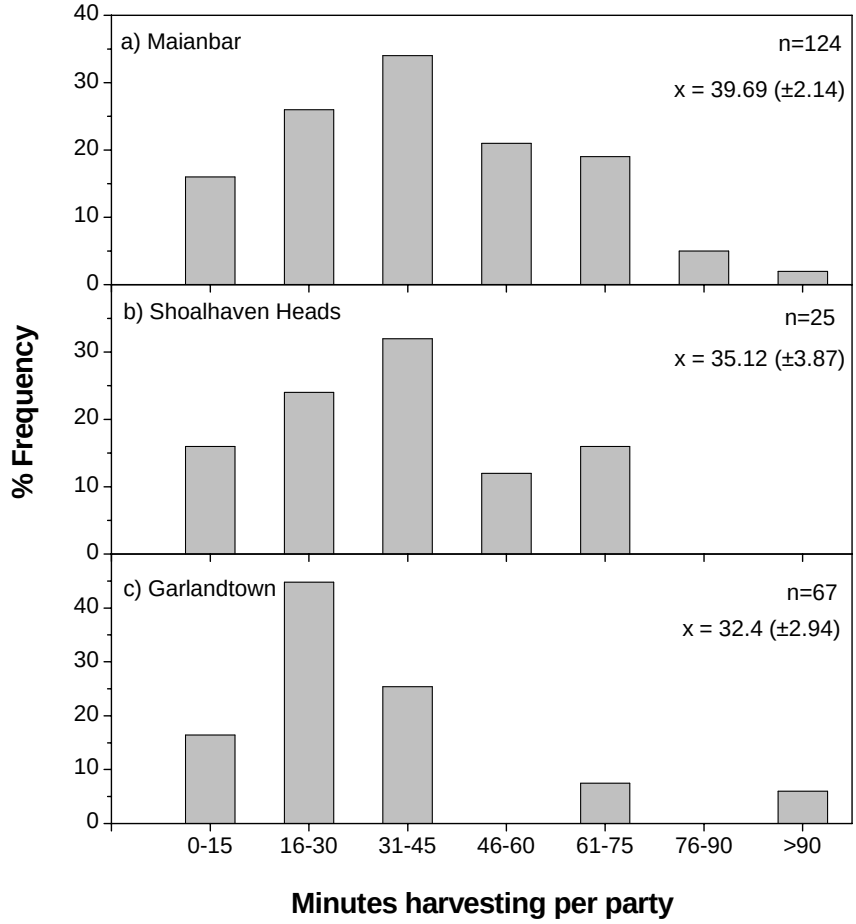


Figure 6.2. Frequency histograms showing the number of minutes spent harvesting *T. australiensis* by recreational bait harvesters at Maianbar, Shoalhaven Heads and Garlandtown, between September 2002 and February 2003.

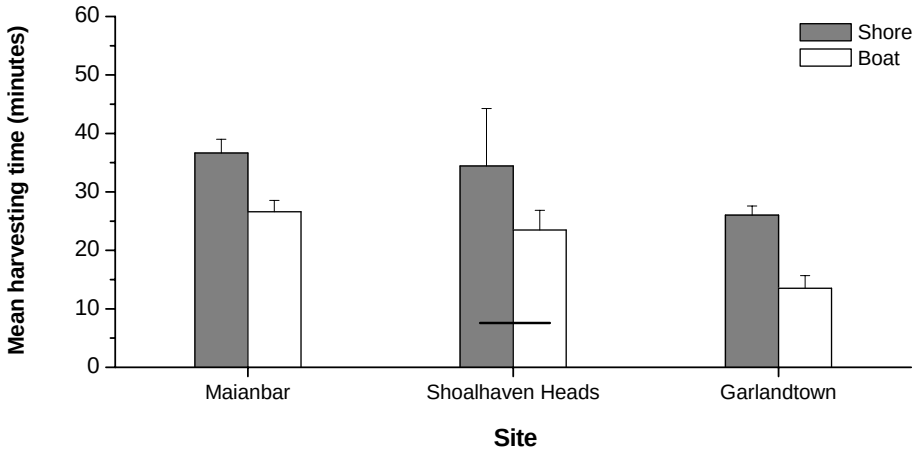


Figure 6.3. Mean harvesting time of shore-based and boat-based harvesters collecting *T. australiensis* for bait at Maianbar, Shoalhaven Heads and Garlandtown, between September 2002 and February 2003. Horizontal lines join pairs of means not significantly different (*t*-tests, $P < 0.05$). Standard error shown.

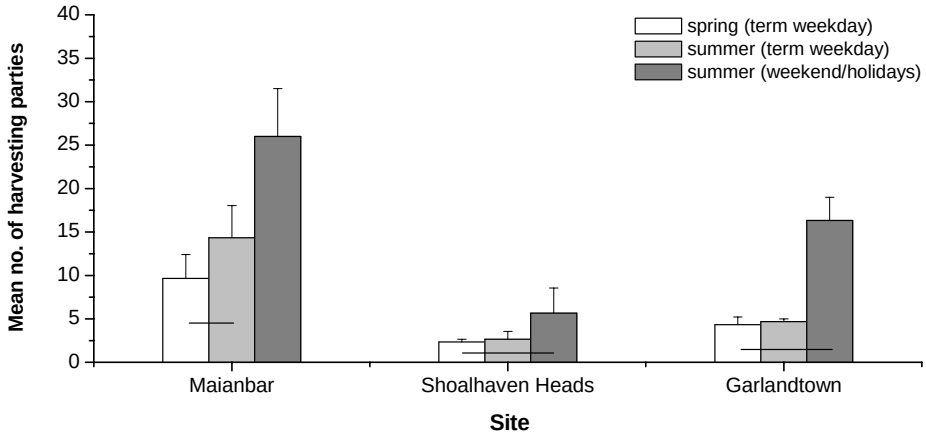


Figure 6.4. Mean number of harvesting parties collecting *T. australiensis* for bait at Maianbar, Shoalhaven Heads and Garlandtown on term weekdays in spring and summer 2002/2003 and on weekends/school holidays in summer 2002/2003. Horizontal lines join pairs of means not significantly different (SNK test, $P < 0.05$). Data transformed to *log* (x+1). Standard error shown.

Table 6.3. Results of ANOVA testing for differences in the mean number of harvesting parties collecting *T. australiensis* for bait between sites (Maianbar, Shoalhaven Heads and Garlandtown) and seasons/days (spring term weekdays, summer term weekdays, summer weekends/school holidays) from September 2002 to February 2003. All factors considered fixed. $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***).

Source	d.f	MS	*F*
Site	2	395.11	17.21***
Season/Day	2	287.44	12.52***
Site x Season/Day	4	37.55	1.64
Residual	17	22.96	
Total	26		

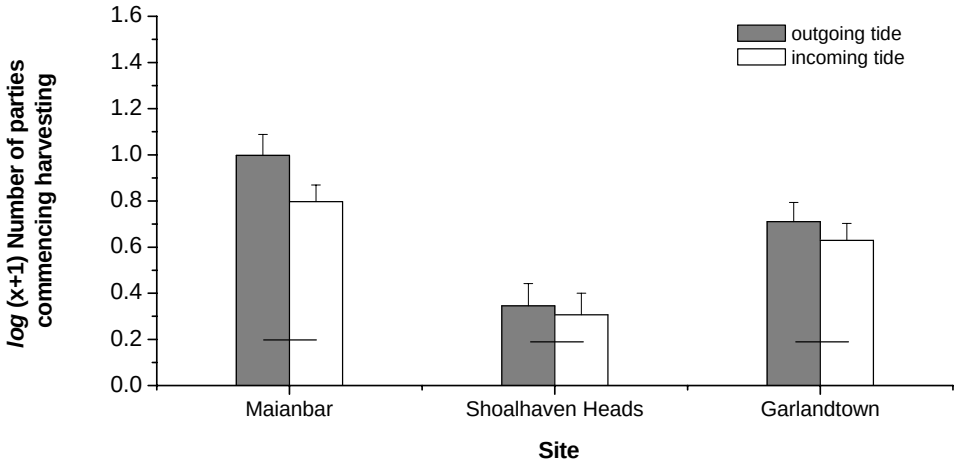


Figure 6.5. Mean number of harvesting parties commencing collecting of *T. australiensis* for bait during outgoing and incoming tides at Maianbar, Shoalhaven Heads and Garlandtown, between September 2002 and February 2003. Horizontal lines join pairs of means not significantly different (SNK test, $P < 0.05$). Data transformed to *log* (x+1). Standard error shown.

Table 6.4. Results of ANOVA testing for differences in the mean number of parties commencing harvesting of *T. australiensis* between tides (incoming vs. outgoing) and sites (Maianbar, Shoalhaven Heads and Garlandtown), between September 2002 to February 2003. All factors considered fixed. $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***). Data transformed to *log* (x+1).

Source	d.f	MS	*F*
Site	2	1.49	22.96***
Tide	1	0.15	2.37
Site x Tide	2	0.03	0.49
Residual	48	0.06	
Total	53		

6.3.2 Harvester interviews

Responses to interview questions are summarized in pie charts (Fig. 6.6). The proportion of people that agreed to participate in the survey was similar across all sites and ranged from 78 to 82% (Fig. 6.6a). The number of parties that avoided the creel clerk, or had been previously interviewed on other occasions, was low. Forty percent of anglers interviewed indicated that they had been harvesting between 31 and 60 minutes (Fig. 6.6b (i)). However, comparisons with creel survey observations showed that only 11% of parties estimated their harvesting time correctly, with 49% of respondents estimating to within 25% of their actual harvesting time, and 32% of people incorrectly estimating their time by 26 – 50% (Fig. 6.6b (ii)). Anglers more commonly overestimated their time spent harvesting, with 55% of anglers overestimating their harvesting time (Fig. 6.6b (iii)).

Catches of *T. australiensis* reported by harvesters varied between sites (Fig. 6.6c). At Shoalhaven Heads and Garlandtown the majority of parties claimed they had caught between 0 - 100 individuals. At Maianbar, harvesters reported much higher numbers, with 69% claiming catches of 100 - 300 or more individuals. Whilst most harvesters over-estimated their harvesting time, the reverse was true when reporting catches. Of the harvesters that allowed direct counting of their catches (n = 28), 76% under-estimated their catch (Fig. 6.6d). Only 22% of people correctly estimated their catches, with 71% of people incorrectly estimating their catch by up to 50%, and 7% of people by more than 50%.

Figure 6.6. Responses of recreational bait harvesters to interview questions regarding collection of *T. australiensis* during surveys at Maianbar, Shoalhaven Heads and Garlandtown between September 2002 and February 2003.

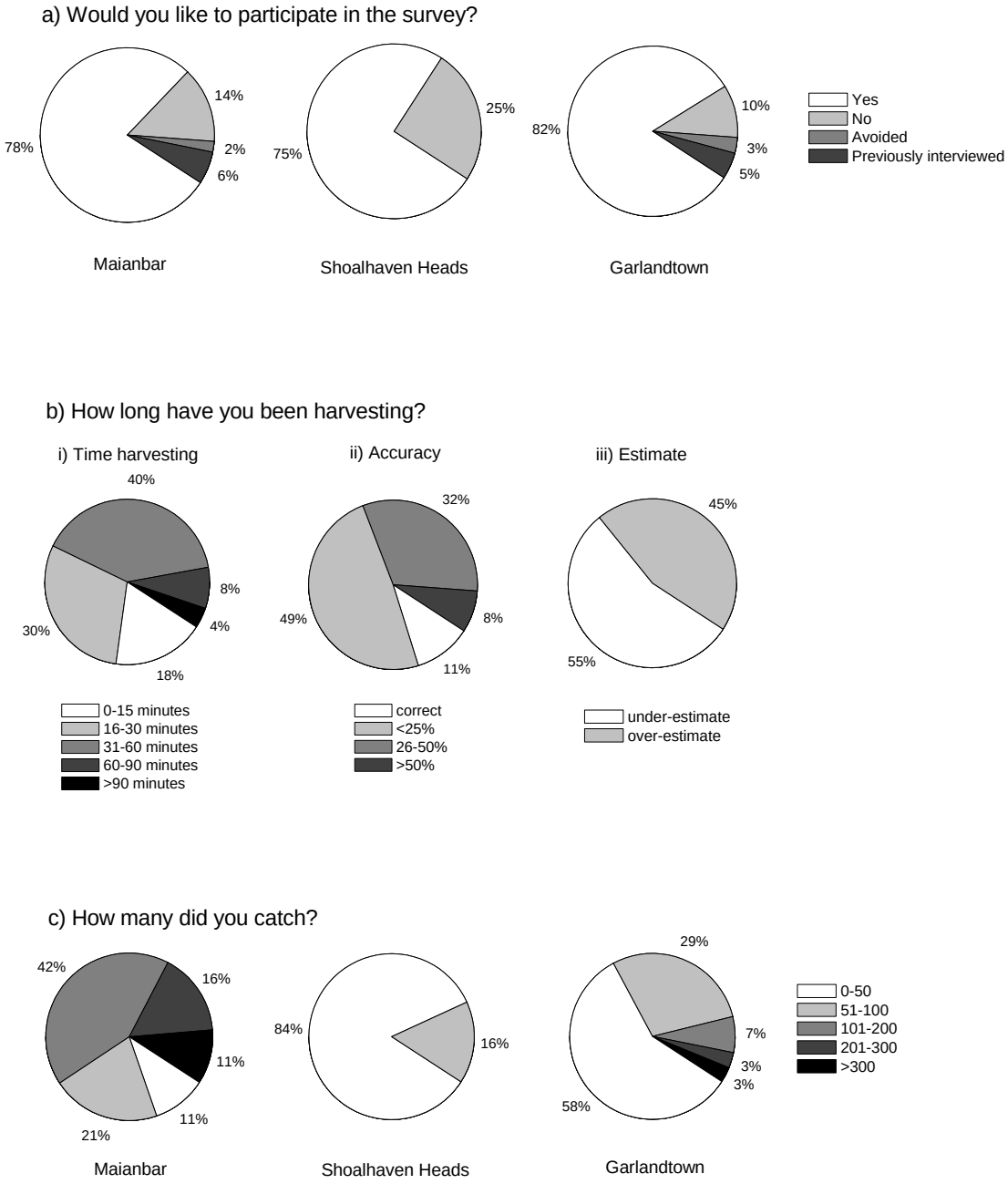
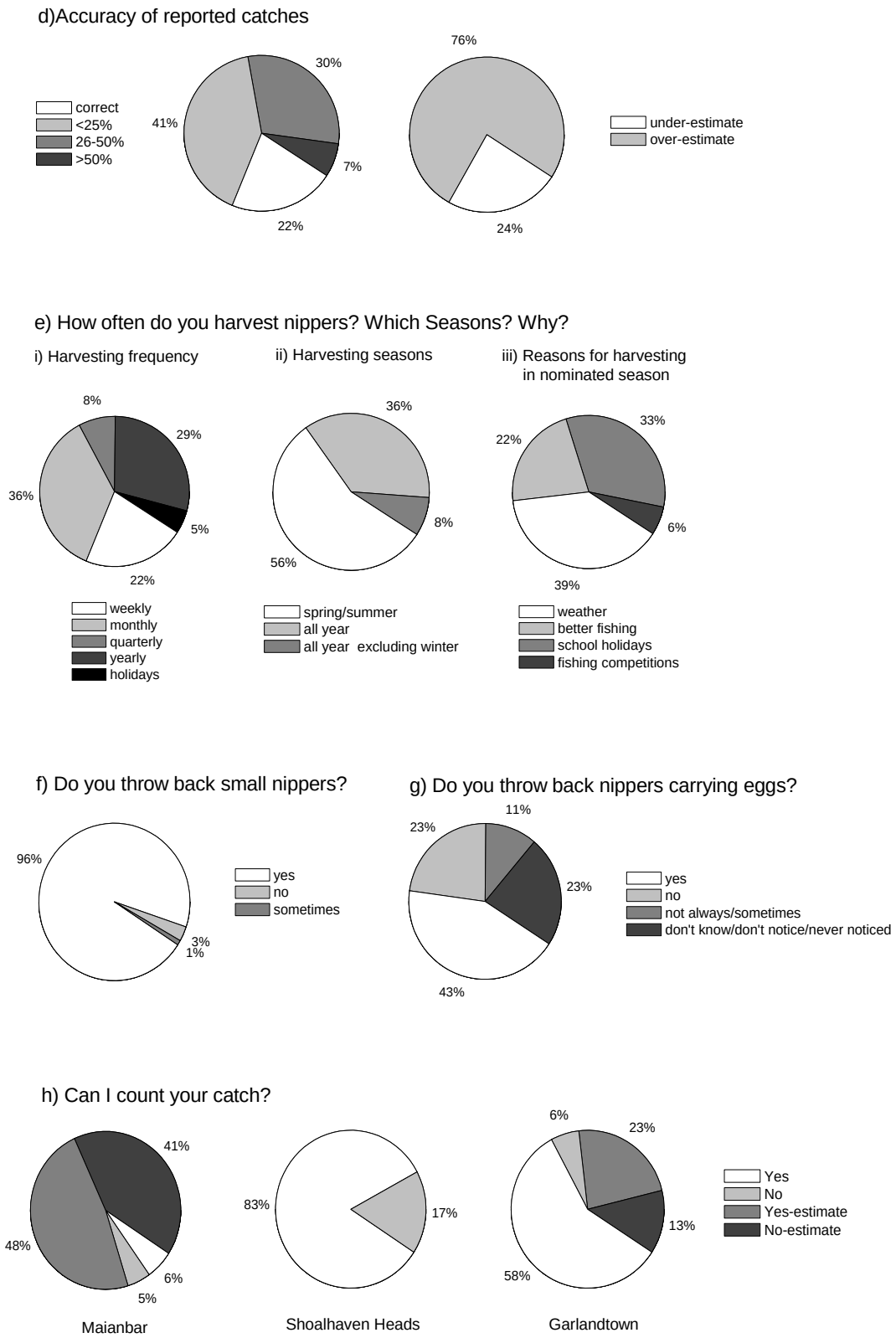


Figure 6.6 Continued



More than half of the parties interviewed harvested either weekly or monthly (Fig. 6.6e (i)). A large percentage of people harvested on a yearly basis with only 5% nominating holiday periods, which may be more frequently than yearly. Most people harvested during spring and summer months (56%), with a relatively large proportion of people (36%) harvesting all year round (Fig. 6.6e (ii)). A small percentage of people (8%) claimed they harvested all year round except winter months. Reasons for harvesting in particular seasons varied, with most people indicating that better/warmer weather in spring/summer was the main factor (6.6e (iii)). Better fishing during warmer months and school holidays were also strong reasons for harvesting. Only 6% of people cited fishing competitions as the reason for harvesting at particular times of the year.

The proportion of harvesters that claimed they discarded small individuals of *T. australiensis* was 96%. (6.6f). However, small individuals were still noted in the catches of many parties that claimed they had discarded them. Only 43% of people discarded ovigerous females and 23% consciously kept them (6.6g). A large proportion of people (23%) claimed they never noticed, do not notice, or do not know about egg-carrying females. Such vague responses were more common at times when females were gravid, and egg-carrying females were frequently noted in the bait buckets of persons that claimed they had not kept them.

The numbers of people that consented to having their catch counted varied between sites (6.6h). Only 6% of people at Maianbar would allow their catches to be directly counted, compared to 83% at Shoalhaven and 58% at Garlandtown. This variation was largely due to the lower numbers of *T. australiensis* caught at

Shoalhaven Heads, which made direct counts rapid. Given the higher catches at Maianbar and Garlandtown, many harvesters would only allow an estimate of their catch without handling due to time constrainers and/or other reasons. Sometimes, the creel clerk was able to gain a look at the catch and estimate numbers even though the harvester had declined to have their catch counted, either directly or by approximation. The small percentage of anglers where no count or estimate was made of catches relates to situations where lids were kept on buckets and/or the catch concealed by the angler.

6.3.3 Harvest estimates

The mean number of *T. australiensis* harvested per party (determined by direct counts and estimates) differed significantly between sites (one-way ANOVA; $F = 12.11$, $P < 0.001$) and was higher at Maianbar compared to Shoalhaven Heads and Garlandtown (SNK tests) (Fig. 6.7). At Maianbar, a large proportion of harvesting parties collected more than 200 individuals per trip, with small percentages harvesting more than 400 animals. Small numbers of people collected more than 200 *T. australiensis* at Garlandtown, however the majority of parties harvested less than 100 individuals, with no catches over 400 animals. In contrast, catches at Shoalhaven Heads were markedly lower than either Maianbar or Garlandtown, with most people collecting less than 50 individuals.

ANOVA revealed significant differences in mean CPUE (number of *T. australiensis*/per minute) between sites (Fig. 6.8, Table 6.5a). Mean CPUE was significantly different between all sites and was higher at Maianbar, followed by

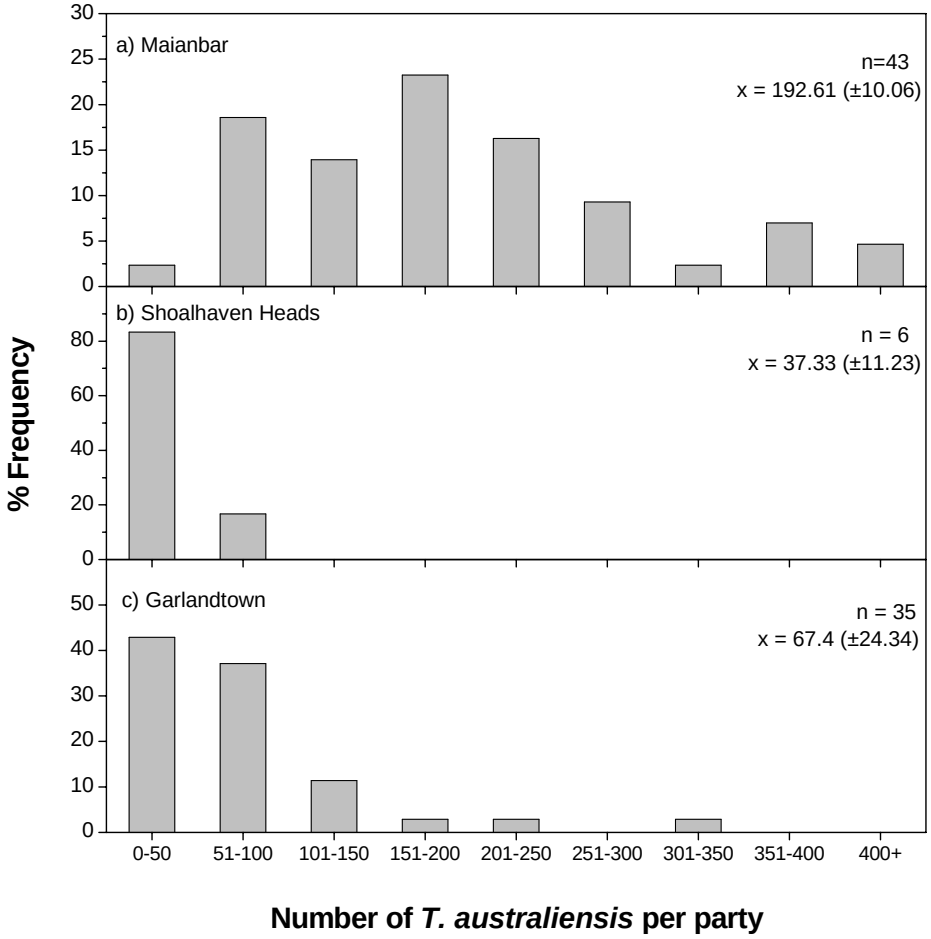


Figure 6.7. Frequency histograms showing the number of *T. australiensis* harvested per party, per trip at a) Maianbar, b) Shoalhaven Heads, and Garlandtown between September 2002 and February 2003. x = mean number of *T. australiensis* harvested per party ± standard error.

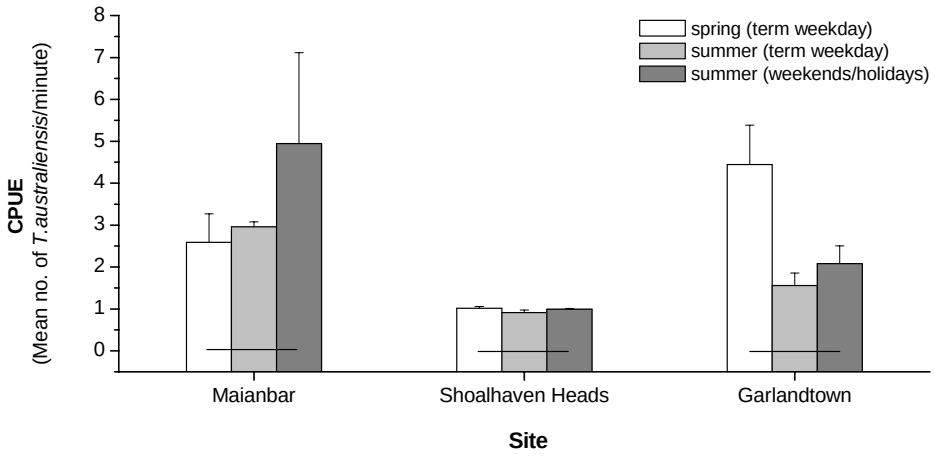


Figure 6.8. Mean CPUE (number of *T. australiensis* per minute) of recreational anglers harvesting *T. australiensis* at Maianbar, Shoalhaven Heads and Garlandtown on term weekdays in spring and summer 2002/2003 and on weekends/school holidays in summer 2002/2003. Standard error shown. Horizontal lines join means not significantly different (SNK tests, $P < 0.05$).

Garlandtown and Shoalhaven Heads (SNK tests). Mean effort (mean number of harvesting minutes per 6-hour low-tide period) differed significantly between sites and season/day-type (ANOVA, Table 6.5b) and was higher at Maianbar, followed by Garlandtown and Shoalhaven Heads (Fig. 6.9). Mean effort was also significantly higher on summer weekends at Maianbar and Garlandtown, but not Shoalhaven Heads even though a similar trend was observed (SNK tests). For the mean daily harvest (CPUE x effort), ANOVA revealed significant differences between sites and season/day-type (Table 6.5c; Fig. 6.10). Mean daily harvest differed significantly between all sites and was higher at Maianbar, followed by Garlandtown and Shoalhaven Heads (SNK tests). A general trend of increased harvests on summer holidays/weekend days was evident, but only significant for Shoalhaven Heads (SNK tests) (Fig. 6.10).

Table 6.5. Results of ANOVA testing for differences in mean CPUE, effort and daily harvest of *T. australiensis* by recreational anglers between sites (Maianbar, Shoalhaven Heads and Garlandtown) and season/day-type (spring term weekdays, summer term weekdays, summer weekends/school holidays) from September 2002 to February 2003. All factors considered fixed. $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***). Daily harvest data transformed to *log* (x+1) to remove heterogeneous variances.

Source of variation	d.f	a) CPUE	b) Effort	c) Daily Harvest
Site	2	7.11**	19.92***	49.79***
Season/Day-type	2	1.07	11.55***	11.46***
Site x Season/Day-type	4	2.28	1.45	0.62
Residual	18			
	27			

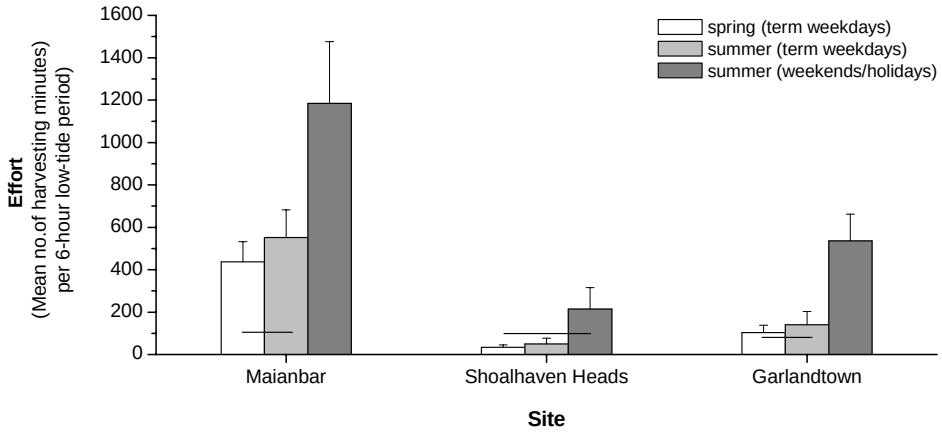


Figure 6.9. Mean effort (number of harvesting minutes per low-tide period (combined for all harvesting parties) of anglers harvesting *T. australiensis* at Maianbar, Shoalhaven Heads and Garlandtown on term weekdays in spring and summer 2002/2003 and on weekends/school holidays in summer 2002/2003. Standard error shown. Horizontal lines join means not significantly different (SNK tests, $P < 0.05$).

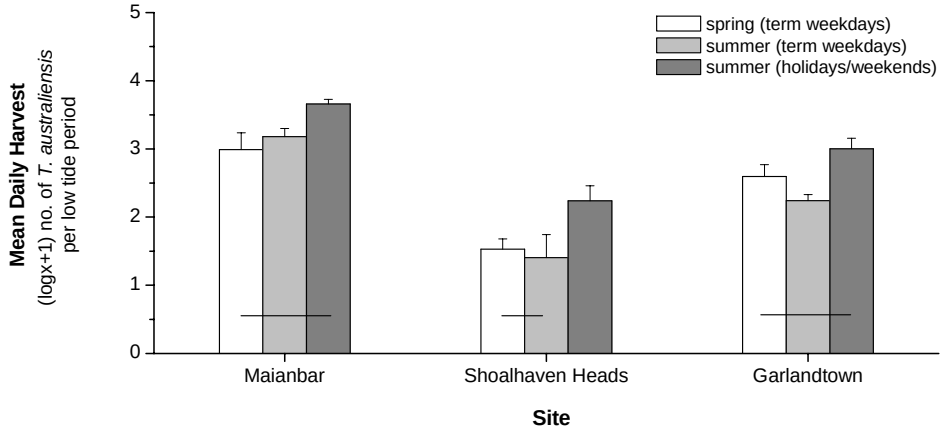


Figure 6.10. Mean daily harvest of *T. australiensis* by recreational anglers during low-tide periods at Maianbar, Shoalhaven Heads and Garlandtown on term weekdays in spring and summer 2002/2003 and on weekends/school holidays in summer 2002/2003. Data transformed to *log* (x+1). Standard error shown. Horizontal lines join means not significantly different (SNK tests, $P < 0.05$).

Estimates of the total catch of *T. australiensis* over the study period varied considerably between sites (Table 6.6). At Maianbar, an estimated 312,334 (±42,712) individuals of *T. australiensis* were harvested by recreational anglers over the 6-month sampling period, which represents approximately 1.98% of the standing stock. Catches were substantially lower at Shoalhaven Heads with 12,624 (±2,818) individuals, representing approximately 0.49% of the standing stock. At Garlandtown the total harvest was much larger at approximately 81,425 (±15,277) animals, which equates to around 1.84% of the standing stock.

Table 6.6. Estimates of mean and total recreational catch (±SE) of *T. australiensis* by day-type stratum season and overall study period at Maianbar, Shoalhaven Heads and Garlandtown, between September 2002 and February 2003. Standard errors calculated according to Pollock *et al*. (1994). Spring weekends treated as spring weekdays (see text).

Site Stratum	Sampling Days (low-tide periods)	Sample mean	Total days (low-tide periods)	Stratum total	SE
Maianbar					
Spring weekdays	3	1256.94	63.76	80,147.4	30,229.3
Spring weekends/hols	Not sampled – treated as spring weekdays				
Total harvest spring				80,147.4	30,229.3
Summer weekdays	3	1624.11	27.53	44,711.7	10,493.9
Summer weekends	3	4682.19	40.04	187,474.9	28,291.7
Total harvest summer				232,186.6	30,175.2
Total harvest (spring and summer)				**312,334**	**42,712**
Shoalhaven Heads					
Spring weekdays	3	37.03	64.06	2,372.1	803.8
Spring weekends/hols	Not sampled – treated as spring weekdays				
Total harvest spring				2,372.1	803.8
Summer weekdays	3	39.43	27.75	1,094.2	598
Summer weekends/hols	3	220.83	41.47	9,157.8	2,694.3
Total harvest summer				10,252	2,700.9
Total harvest (spring and summer)				**12,624**	**2,818**
Garlandtown					
Spring weekdays	3	460.11	63.03	29,000.73	11,037.57
Spring weekends	Not sampled – treated as spring weekdays				
Total harvest spring				29,000.73	11,037.57
Summer weekdays	3	181.37	27.69	5,022.13	1,059.97
Summer weekends/hols	3	1131.85	41.88	47,401.88	10,508.26
Total harvest summer				52,424.01	10,561.59
Total harvest (spring and summer)				**81,425**	**15,277**

6.4 Discussion

Small numbers of fish or invertebrates are generally taken by recreational anglers on individual fishing trips (Hilborn, 1985; Underwood, 1993a; West and Gordon, 1994). The present study has shown the reverse for *T. australiensis*, with individual harvesting parties at some sites frequently collecting several hundred animals (Fig. 6.7). In fact, at Maianbar in Port Hacking, the mean number of *T. australiensis* per party was almost 200 individuals, with one party collecting approximately 1,000 animals in one trip. Whilst individual catches were quite large at the former site, harvests were considerably lower at Shoalhaven Heads and Garlandtown, with means of 37 and 67 animals per party respectively. Such marked geographic differences in mean catch per party were generally related to the lower fishing quality (CPUE) at these sites, as mean harvesting times were not significantly different between locations (Fig. 6.2). Although *T. australiensis* was more abundant at Garlandtown than at Maianbar in the fishery-independent surveys (see Chapter 3), the lower abundance of bait-sized individuals at the former site was due to the smaller size range of the population, and may explain the lower CPUE at this location.

In Moreton Bay (Queensland), McPhee and Skilleter (2002b) found similar results to the present study, with mean harvesting times of 27 - 37 minutes per party and CPUE's of 2 - 2.6 individuals per minute. However, few parties harvested more than 200 individuals of *T. australiensis* per trip in Moreton Bay, which differs to the results at Maianbar and Garlandtown in the present research (Fig. 6.7). This difference may be related to the fact that McPhee and Skilleter (2002b) interviewed a large proportion of competitors in a fishing tournament, who were

presumably of greater experience than average anglers, requiring fewer animals to catch more fish. Although, differences in the mean number of animals harvested per party between competitors and non-competitors were not significant. In addition, the sites sampled by McPhee and Skilleter (2002b) primarily require access via boat and therefore, may have only included interviews of boat-based anglers. In the present study, boat-based harvesters spent significantly less time harvesting than shore-based anglers at most sites (Fig. 6.3), and would have caught smaller numbers of animals, for immediate use within the estuary. Shore-based anglers that arrived at sites by car or foot frequently indicated that they were fishing the next day, in many cases at different bodies of water many kilometres from the harvesting site. Consequently, many shore-based parties stated they collected higher numbers of shrimp to compensate for overnight mortality, which may be large. Also, many shore-based anglers indicated they were collecting additional shrimp for other individuals (family members or friends) that were not present during the harvesting activities, but would be sharing the bait whilst angling for finfish at a later time and/or different place.

The high level of refusal of anglers consenting to have their catches counted at some sites in the present study was similar to the results of McPhee and Skilleter (2002b). They found that fewer than 50% of parties would allow their catches to be directly counted. In the present study, the proportion of people consenting to having their catch directly counted ranged from 6 to 83% and was particularly low at the Maianbar site (Fig. 6.6h), where catches were large and took a significant amount of time to count. Many anglers objected to having their catch handled but would allow visual estimates of their harvest. Yet, the proportion of people that

would not allow their catch to be counted by any method was also quite high (19 - 46% at some sites, Fig. 6.6h). The reluctance of people to participate may result from confusion surrounding bag and size limits, which do not actually apply to *T. australiensis*, but are assumed to by many anglers. In fact, this reason may account for the high numbers of people that refused to take part in interviews (6.6a). Such high refusal rates are uncommon for creel surveys of finfish (e.g., West and Gordon, 1994), where bag limits are more explicit and catches comparably lower, taking little time to measure. Underwood and Kennelly (1990) also working in NSW, found that only 0.05% of people were uncooperative in a creel survey conducted on rocky shores, where bag limits for many species did not exist. Greater awareness over the lack of bag limits may improve compliance in future surveys, but may also result in larger catches.

Harvest estimates reported by anglers may remove the need to handle catches and undertake direct counts. However, the present study found that many anglers incorrectly estimated their catch and more commonly underestimated numbers (Fig. 6.6d). Anglers in Moreton Bay (Queensland), also underestimated catches of *T. australiensis* (McPhee and Skilleter, 2002b). The use of angler estimates of harvest for *T. australiensis*, both in on- and off-site surveys should therefore be avoided, as the recall bias of anglers would presumably get worse hours, days or weeks after the event (Pollock *et al.*, 1994). A novel approach to estimating the harvest of *T. australiensis* by individual anglers was tested by McPhee and Skilleter (2002b). They counted the number of times a harvester (or helper) picked up a shrimp from the sediment (called a peck). This method had the distinct advantage of not needing to interview harvesters and proved to be quite accurate

(94% - 98%). However, large numbers of harvesting parties operated on sandflats during low-tide periods in the present study and large numbers of observers would be required to estimate harvests using this method. The cost of employing large numbers of observers to watch each individual party would prove prohibitive for many sampling programs. A further disadvantage of this methodology, as pointed out by the authors (McPhee and Skilleter, 2002b), is that it does not provide size frequency data. Obtaining size frequency information was also difficult in the present study and eventually abandoned, given the reluctance of anglers to have their catch handled and the need to immobilize or anaesthetize animals to get accurate measurements. The use of direct counts of angler harvests is advocated for future creel studies on *T. australiensis*. However, increasing the proportion of anglers that are willing to having their catch counted and obtaining representative and accurate size measurements of harvested individuals, still presents challenges.

Despite a strong awareness against retaining undersized individuals, harvesters often still had small animals in their catches, particularly at Garlandtown, where sizes of animals were generally smaller (see Chapters 4 and 5). Many harvesters are size selective not only for conservation purposes, but from a bait quality perspective, as very small animals are not considered good bait (pers. comm.). Also, small individuals (<5 mm) are often very difficult to detect in the spoils of the yabby pump without the use of a sieve. No quantitative data are available on size ranges of catches from the present research. Data from previous studies (McPhee and Skilleter, 2002b) support the hypothesis that harvesters of *T. australiensis* are size selective, as a very low proportion of catches measured from Moreton Bay were less than 9 mm CL. Studies of other species have also shown

anglers to be size selective (Wynberg and Branch, 1991). Perhaps of greater concern, is the fate of discarded shrimp that are not covered with sand or returned to burrows. At Langebaan Lagoon in South Africa, 55% of *C. kraussi* discarded by bait-harvesters were preyed upon by opportunistic kelp gulls (*Larus dominicanus*) (Wynberg and Branch, 1991). Gulls were often observed following harvesters and consuming discarded shrimp in the present study and in previous investigations (McPhee and Skilleter, 2002b). A greater consciousness of predation by gulls on undersize shrimp and methods of protection, such as releasing individuals into finger-sized holes in the substrate and covering with sand is recommended. Similarly, many anglers were unaware of egg-carrying females (Fig. 6.6g), despite large numbers of gravid females at all sites during the summer months.

The present research indicates that the recreational harvest of *T. australiensis* during individual low-tide periods may be considerable. For example, on summer weekend/holidays, the mean estimated catch from Maianbar exceeded 4,500 individuals over a 6-hour low-tide period (Table 6.6). In comparison, McPhee and Skilleter (2002b) estimated that participants in a fishing tournament extracted approximately 3,900 individuals of *T. australiensis* over an entire week. In South Africa, anglers removed over 1 million individuals (3.2% of total stock) of *C. kraussi* per annum in Langebaan Lagoon (Wynberg and Branch, 1991) and 1,860,000 individuals (8.5% of total stock) of *U. africana* from the Knysna Estuary (Hodgson *et al*., 2000b). In Paraná State Brazil, bait harvesters removed an estimated 251,041 individuals (10% of total stock) of *Callichirus major* from an 11 km stretch of sandy beach (Souza and Borzone, 2003). Estimates of total

catch over the 6-month period examined in the present study ranged from tens of thousands at Shoalhaven Heads and Garlandtown, to hundreds of thousands at Maianbar (Table 6.6). An estimated 312,334 individuals were harvested over the 6-month sampling period for the latter site and a number of other popular sites occur in Port Hacking. Yet the estimate from the National Recreational and Indigenous Fishing Survey for the entire Port Hacking was 36,874 individuals of *T. australiensis* (Gary Henry, NSW Fisheries unpublished data). Estimates of 37,600 individuals per annum for the Shoalhaven River by the National Recreational and Indigenous Fishing Survey (Gary Henry, NSW Fisheries unpublished data), appear more accurate. Although this figure may also be an underestimate, considering 12,624 animals were estimated to be harvested in a 6-month period at Shoalhaven Heads in present study, and a number of other popular harvesting sites exist in this river. No data was available from the National Recreational and Indigenous Fishing Survey for Moruya alone (Gary Henry, pers. comm).

The large discrepancies between estimates from telephone and diary based surveys of the National Recreational and Indigenous Fishing Survey (Henry and Lyle, 2003) and the present study are not surprising, considering the inaccuracy of anglers in recalling their catches and the apparent predisposition to underestimate total numbers harvested, following only short periods after fishing (Fig. 6.6d). This highlights the inadequacy of relying on large-scale angler surveys alone to estimate harvests of target species and frame conservations measures. Where possible, results should be validated through field-based observations at a number of locations, as in the present research.

Whilst the magnitude of the harvest of *T. australiensis* appears significant for some sites such as Maianbar, the total harvest for the 6-month period represents fewer than 2% of total standing stock across all locations. It must also be stressed that these estimates are considered to be minimums, since harvesting undoubtedly occurs outside of the hours examined in the present study (i.e., before 9am and after 6/7pm) and because weekends were treated as weekdays for spring months in the total catch estimates, due to insufficient number of low-tide periods for sampling. Further research is also required to determine harvests in autumn and winter. Since only 36% of people claimed to harvest all year round (Fig. 6.6e) a doubling of these estimates for an entire year is probably an overestimate. Furthermore, previous studies on rocky shores and sandy beaches in NSW have shown that fewer people harvest for bait during winter months (Underwood, 1993a; Murray-Jones and Steffe, 2000). Even if the total catch at Maianbar was 1 million animals per annum, this would still only represent approximately 6% of the standing stock based on standing stock estimates of the present study (see Chapter 3). Continued monitoring of these sites is required as population estimates may be considerably lower during years without severe drought (see discussions in Chapter 3 and 4). The question of whether current levels of harvesting are ecologically sustainable in the long-term cannot be answered here and further research is required.

Investigating ecological sustainability not only requires information on catch and effort but also data on the effects of harvesting on target organisms and communities, which can only be achieved through controlled manipulative experimentation (Underwood, 1993b). An experimental approach is also required

to assess the effectiveness of management strategies such as bag and size limits on populations. This presents a number of challenges for researches examining *T. australiensis* in NSW. Firstly, finding unharvested control sites is difficult since there are few sites if any, which are completely closed to harvesting. Also, many closed sites may be still affected by humans unless effective physical barriers and signage are implemented (Keough and Quinn, 2000). Closing popular harvesting sites over long periods for manipulative experiments in NSW is difficult and unpopular in the short-term. Certainly, comparing less-harvested sites or closed areas in marine reserves with more harvested sites is an option. Yet, data on catch and effort from a greater number of sites is required, as locations that appeared to be intensively harvested prior to the present study, such as Shoalhaven Heads, actually had relatively low levels of catch and effort (Figs. 6.9 and 6.10).

An alternative approach to examining ecological sustainability of harvesting in soft-sediments has involved conducting manipulative experiments, where individual plots within sandflats are depopulated to measure effects on population and community structure (Jackson and James, 1979; McLusky *et al.*, 1983; Cryer *et al.*, 1987; Wynberg and Branch, 1994). Using similar approaches, previous studies demonstrated that bait-pumping for *C. kraussi* and *U. africana* in South African estuaries, had the same effect on target populations and infaunal communities as trampling (Wynberg and Branch, 1994, 1997). It was hypothesised that the prolonged recovery time for shrimp and other taxa were caused by modifications to sediment properties including collapsing of burrows, compaction of sediment and reduction of oxygen. Recently, Contessa and Bird (2004) confirmed the above hypotheses using BACI type experiments

(Underwood, 1993b) in southern Australia. They showed that disturbances associated with bait-pumping for *T. australiensis* in Western Port (Victoria), modified sediment properties including porosity and created anoxic conditions. However, data presented on the effects of harvesting on populations of shrimp are less convincing. For example, Contessa and Bird (2004) estimated population densities of *T. australiensis* before and after disturbances using burrow counts, which are unreliable for *T. australiensis* in Queensland (McPhee and Skilleter, 2002a) and in south-eastern Australia (see Chapter 3 in present study).

While the experiments described above suggested that densities of *T. australiensis* may be reduced through bait collection activities in the short-term (i.e., 3 months) (Contessa and Bird, 2004), recovery and sustainability of populations over longer time scales is still unknown. Indeed, future manipulative studies should be conducted over wider spatial and temporal scales and employ quantitative sampling methods (as in Chapter 2). However, the use of destructive methods does confound the effects of sediment disturbance and removal of animals *per se* on populations and communities. Although, it has already been established that disturbance from pumping activities may be just as deleterious to populations of *C. kraussi* (Wynberg and Branch, 1994, 1997) and *T. australiensis* (Contessa and Bird, 2004), as the removal of actual animals. The problem of defaunating areas of sandflat large enough to prevent shrimp immigrating back into experimental plots, combined with sampling sufficient numbers of areas to avoid pseudoreplication (given the labour intensive treatments), has been recognised (Wynberg and Branch, 1994). Since the magnitude of populations at sites in the present study were estimated to be in the order of millions, removal of *T.*

australiensis would need to be significant to detect any change beyond natural variability in time and space (see Chapter 3), which involves a number of ethical and ecological considerations. Comparisons with areas that are closed to harvesting such as marine reserves, is perhaps the most practical direction for future studies seeking to determine the ecological sustainability and wider ecosystem effects of recreational harvesting of ghost shrimp, including *T. australiensis*. However, a lack of suitable locations within the current framework of marine reserves in NSW at present, prohibits sufficient replication for "Beyond BACI" type experiments (after Underwood, 1994).

The present research has provided information for the conservation and management of *T. australiensis*, by describing the characteristics, extent and intensity of harvesting at selected sites in south-eastern NSW. The data suggest that although seemingly large numbers of *T. australiensis* were harvested by individual parties from some sites (e.g., Maianbar) on particular days (e.g., weekends and holidays), estimates of total recreational catch may represent fewer than 4% of total stock sizes per annum across locations. Furthermore, considerable geographic variations in harvests exist between sites, which is probably a result of lower abundances at some sites (see Chapter 3) and hence, a lower catch per unit effort. Finally, discrepancies between total harvest estimates from the present study and unpublished data from the National Recreational and Indigenous Fishing Survey (Henry and Lyle, 2003), highlights the inadequacy of relying primarily on off-site surveys to determine levels of harvesting, as well as the importance of on-site validation, carried out at appropriate spatial and temporal scales. Results of the present study are further discussed in Chapter 7,

which also considers the conservation and management of *T. australiensis* in NSW and outlines future research priorities.

Chapter 7

Conclusions and recommendations

7.1 Introduction

This chapter outlines the major findings of research contained in each chapter of this thesis. An overview of the life-history of *T. australiensis* in south-eastern Australia is postulated, and results are discussed in relation to management and conservation of the resource, as well as directions for future research.

7.2 Comparison of methods for sampling *T. australiensis*

The objectives of this study were to develop and compare two different quantitative methods of sampling *T. australiensis* based on coring and pumping. It represents the first study to compare the selectivity and efficiency of methods commonly used to sample burrowing thalassinid ghost shrimp.

Major findings

- Suction pumps (i.e., yabby pumps) were a more efficient method of sampling *T. australiensis* compared to sampling with cores, allowing greater replication in experimental designs.
- Catches from yabby pumps represented a wider range of ghost shrimp, from newly recruited individuals through to large adults.
- Female-biased sex ratios from yabby pump catches are characteristic of thalassinid populations, and are more likely to represent real sex ratios through increased sample size, rather than method-based selectivity.

7.3 Spatial and temporal patterns of distribution and abundance of *T. australiensis*

This study is the first to quantitatively sample populations of *T. australiensis* (and perhaps any other thalassinid), using a hierarchical nested sampling design over multiple spatial and temporal scales, and over a wide geographic range. The experimental design incorporated nested spatial scales which ranged from metres (between quadrats), tens to hundreds of metres (between plots), and kilometres (between sites within estuaries). Sampling was conducted on a monthly basis across all spatial scales for the first year and quarterly for the second year. One site (Maianbar) was sampled approximately monthly for the entire two-year period to investigate differences in abundance between years, with respect to the amount of variation between months within years. Since previous studies have often used burrow counts as a surrogate estimate of abundance for thalassinid shrimp, another aim of this chapter was to investigate the relationship between burrow openings and abundance of *T. australiensis*. A final aim was to estimate the magnitude of populations at each sampling location.

Major findings

- Abundances of *T. australiensis* were generally more variable across smaller spatial scales such as between sites within estuaries (1 - 2 km) and within sites (tens to hundreds of metres), than across large spatial scales between estuaries (hundreds of km).
- Variation in spatial patterns over time suggested that *T. australiensis* may form spawning aggregations during spring/summer periods.

- Recruitment occurred during spring/summer periods and commenced earlier in southern estuaries. Despite this, the supply of new recruits was still more consistent across large spatial scales such as between estuaries, than on small spatial scales within and between sites within an estuary. These results suggest that transport of larvae within estuaries, selective settlement and post-larval mortality are important factors determining recruitment. An increase in recruitment strength in each consecutive year of the study may be related to an extended drought period, providing favourable conditions for settlement and survival of larvae.

- Even though significant positive relationships between burrow openings and relative abundance were found for *T. australiensis*, the proportion of variation in abundance explained by the number of burrows was generally low. Furthermore, the relationship depended on the particular time and site in question. These results cast doubt on the reliability of burrow counts to provide accurate assessments of population densities.

- Even though relationships existed between burrow openings and abundance of *T. australiensis*, low R^2 values indicated that relationships were generally poor. Furthermore, significant spatial and temporal differences and the interaction of these factors (ANCOVA), suggests that using burrow counts as indirect assessments of population densities may be unreliable.

- The magnitude of populations at most sites was in the order of millions of animals.

This study raises further questions for researchers and provides important directions for future investigations of shrimp abundance and experimental studies

seeking to identify causal processes, which may explain patterns observed in this study. Further studies on patterns of thalassinid shrimp abundance should attempt to sample quantitatively over a range of scales similar to the present study. In fact, studies should seek to include more replication at smaller spatial scales, which were most variable in the present study. Additionally, future investigations of *T. australiensis* should attempt to answer the following questions (listed in order of priority), which have not been resolved in the present study, through a combination of both observational and experimental techniques:

1. Are the spatial and temporal patterns observed in the present study consistent over long-term scales (i.e., 5 to 10 years)? Do similar patterns exist in other regions of Australia and/or for other species of burrowing shrimp in different parts of the world?
2. Do spring/summer breeding aggregations, hypothesised in the present study occur? If so, what stimuli initiate such behaviour and what is the significance for mating systems? Is such behaviour consistent for other species and those that reproduce in cooler seasons and/or all year round?
3. What factors determine variations in recruitment between years?
4. What factors determine variation in recruitment of *T. australiensis* across small scales within estuaries? What are the roles of larval transport, selective settlement and post-larval mortality?

7.4 Reproductive biology of *T. australiensis*

This chapter presents baseline data on the reproductive biology of *T. australiensis* over multiple spatial and temporal scales in south-eastern NSW. Specifically, intra-specific variability in the sex ratio of populations, female size at maturity, commencement and duration of breeding seasons, size-specific fecundity and egg size were investigated. Knowledge of these parameters are necessary for consideration of management strategies such as minimum size limits, restriction on collection of ovigerous females and protection of breeding stocks in marine reserves.

Major findings

- Females were consistently ovigerous during mid-summer and autumn months. However, commencement of the breeding season was asynchronous, with populations in southern estuaries carrying eggs earlier than individuals in northern populations. A similar trend is evident for the whole of eastern Australia when data from previous investigations are also considered.
- Latitudinal variation was also demonstrated for female size at maturity, with females from southern estuaries ovigerous at smaller sizes than individuals from northern populations.
- *T. australiensis* employs a strategy of high fecundity and small egg size compared with other thalassinid shrimp.
- Fecundity increased linearly with female size and was higher for females carrying late stage “eyed” embryos than freshly extruded uneyed eggs. These

relationships differed between populations, although number of eggs per female was not significantly different between sampling locations.

Studies on the reproductive biology of *T. australiensis* described in this thesis, have not only provided information relevant to management of the species, but also the context and basis (after Underwood, 2000) to further examine processes determining observed patterns, using both experimental and mensurative approaches. In recognising the need to understand patterns and processes, further research relating to the reproductive biology and ecology of *T. australiensis* and other burrowing shrimp, has been prioritised into the following areas:

1. Determining the roles of predation, migration and agonistic behaviour in producing female-biased sex ratios in mature size classes of shrimp populations.
2. Investigating latitudinal differences in the commencement of breeding seasons, size at maturity and reproductive output (e.g., fecundity and egg size) throughout the entire range of the species.
3. Examining the roles of environmental factors including temperature, food, population density and salinity in determining size at maturity, commencement and duration of breeding seasons and reproductive output.
4. Investigating the duration of larval development at various temperatures and examining the role in controlling early breeding seasons at higher latitudes.

5. Quantifying the number of broods per season carried by females through field based experimentation (after Tamaki *et al.*, 1996).

7.5 Relative and absolute growth of *T. australiensis*

Prior to this study, data on relative and absolute growth parameters of *T. australiensis* was limited to a single embayment in southern Queensland. The multi-scale analysis of growth in the present study is a novel approach for *T. australiensis* in Australia and for other thalassinids worldwide. Certainly, it is the first study of *T. australiensis* to attempt to determine growth parameters using electronic length frequency analysis (ELEFAN), despite questions regarding the appropriateness of this approach.

Major findings

- Size at maturity as determined from analysis of relative growth was significantly related to latitude for both males and females, with populations in southern estuaries maturing at smaller sizes than those in estuaries further north. This result supports a similar finding for sizes at maturity estimated from ovigerous females (see above). Based on analyses of relative growth parameters, males appear to reach sexual maturity (i.e., a puberty moult) before females.
- The enlarged primary chela possessed by male *T. australiensis* results from differences in allometric growth between sexes following maturity.
- Despite shortcomings and preliminary nature, results from electronic length frequency analysis indicate that *T. australiensis* is a fast growing species with a

life-span of 3 to 4 years. However, results indicating a much longer life-span for some sites are probably an artefact of the ELEFAN procedure.

- Latitudinal differences in VBGF growth parameters were inconsistent between sites within estuaries and between estuaries.
- Exploitation ratios derived from stock assessment based on growth parameters derived from ELEFAN procedures suggest that populations across all sites are currently under-exploited or nearing optimal harvesting rates. However, caution is required in the interpretation of these results for management purposes.

Further research is necessary to investigate the roles of temperature, food and population densities in determining size at maturity and growth of *T. australiensis* and other thalassinids (see Chapter 4). While males matured at smaller sizes than females, hypotheses are speculative at this stage and further research examining reproductive condition of male shrimp is suggested. Additional research on maintaining individuals of *T. australiensis* in aquaria over extended periods is also required to provide estimates of moult increment and frequency. This may allow further development of internal tagging methods in aquaria and in-situ (see Appendix 1) and lead to more accurate descriptions of growth, which do not rely on length-based methods.

7.6 Recreational harvesting of *T. australiensis*

The aim of this study was to investigate the extent and intensity of small-scale harvesting of *T. australiensis* at three selected sites in south-eastern NSW, during spring and summer periods. An unusual outcome from this study was the high rate of people refusing to participate in the research. Furthermore, many parties refused to have their catches handled due to the fragility of the organism and time constraints. Prior to this research, estimates of catches for individual harvesting parties at specific sandflat locations were not available.

Major findings

- Individual anglers and parties frequently harvested large numbers of *T. australiensis* during low-tide periods from sandflat locations, with geographic differences in catch per unit effort (CPUE) related to fishing quality. The combined catch of harvesters was also large, with mean estimated catches at Maianbar during summer weekend/holidays exceeding 4,500 for single 6-hour low-tide periods.
- The majority of anglers frequently over-estimated their time spent harvesting and under-estimated their catches. Data from large-scale telephone and diary-based surveys are therefore likely to underestimate extent and intensity of harvesting at individual locations, given the recall bias of anglers after even short periods.
- Patterns and characteristics of harvesting differed significantly between sites and seasons.

- Estimates of total catch of *T. australiensis* over the 6-month study period varied between sites and although considerable, represent fewer than 2% of estimated stock sizes at each location.

Further monitoring studies incorporating experimental manipulative procedures are required to investigate long-term sustainability of harvesting on target populations and ecosystem components.

7.7 Overview of the postulated life-history of *T. australiensis* in south-eastern Australia

The following section provides an overview of the postulated life-cycle of *T. australiensis* in south-eastern Australia based on the results of field studies described in chapters of this thesis and previous investigations in other regions.

During spring months in south-eastern Australia, increases in water and air temperatures may increase mobility of *T. australiensis*, providing cues to form breeding aggregations through subsurface migrations within sandflat habitats. Details of copulation are unknown for *T. australiensis* and for thalassinid shrimp in general. These hypothesized spawning aggregations result in homogenous distributions on small spatial scales within sandflats (i.e., < 10 m), suggesting animals do not migrate large distances. Across larger scales within sandflats (i.e., tens to hundreds of m), distributions become increasingly patchy as a result of aggregations on small spatial scales.

Ovaries of *T. australiensis* show increased development through spring and summer months. Ovigerous females occur in a unimodal breeding period from mid/late summer through to autumn. However, the appearance of gravid females is asynchronous along a latitudinal gradient, with females from southern estuaries extruding eggs progressively earlier than females from northern estuaries. Breeding lasts approximately 5 to 6 months and although number of broods per female was not experimentally investigated; theoretical maximums of between 3 and 5 broods (with at least two) per female are suggested. Aquarium observations in the present research and from other studies suggest *T. australiensis* incubates eggs for approximately six weeks.

T. australiensis employs a strategy of relatively high fecundity and small egg size compared with other species of burrowing shrimp. Fecundity increases with decreasing latitude and female size, and number of eggs per female ranges from 63 to 4,738. However, differences in fecundity at small spatial scales may be as large as variation across larger scales between estuaries and may be influenced by local environmental conditions and population dynamics. Embryo size does not differ significantly over large geographic scales, but does appear to be related to shrimp size, with larger shrimp producing larger eggs.

After hatching, pelagic larvae are released into the water column as part of the zooplankton, settling within either the same estuary or being transported into coastal waters by tidal processes. The pattern of earlier breeding observed in southern regions may compensate for slower larval development and growth due to lower sea surface temperatures, ensuring that settlement and recruitment occurs

synchronously along the coastline during spring and summer periods, when conditions are favourable. This dispersal strategy may explain the widespread distribution of *T. australiensis* in eastern Australia.

The development time of larvae has not been determined experimentally for *T. australiensis*. The presence of newly settled post-larval recruits (≤ 5 mm, CL) during spring and summer periods suggests that *T. australiensis* may have a larval phase as long as 6 months, which is one of the longest development times for the Thalassinidea and may again explain the widespread distribution in eastern Australia. Larval supply is relatively consistent over large geographic scales such as between estuaries during spring and summer periods and appears to be influenced by large-scale oceanic processes. Within estuaries, local hydrology and environmental factors may affect the supply of larvae between sites, creating patchiness at smaller scales within sandflats. Following settlement, survival of individuals may be controlled by environmental factors such as salinity, as well as other processes such as predation and competition.

Following settlement of larvae during spring and summer months, growth of *T. australiensis* is rapid, with individuals reaching sexual maturity and reproducing after a period of approximately one year. Growth of males and females is similar up until sexual maturity, with males undergoing a puberty moult at smaller sizes than females. Whilst size at maturity for both males and females appears to be related to latitude, the roles of density-dependent and environmental factors in determining these patterns are unclear.

Following sexual maturity, growth of the primary chela becomes increasingly allometric for males and negatively allometric for females, resulting in different sized and shaped chelae. The absence of an enlarged chela for females may be due to the investment of energy into egg production (Felder and Lovett, 1989). For males, development of an enlarged primary chela may serve a specific behavioural function such as grappling with other males during aggressive encounters and mating, and not simply the result of lower reproductive demands. Details on the frequency and duration of moult and intermoult periods after the critical puberty moult are unknown. A life-span of 3 to 4 years is estimated for *T. australiensis* in south-eastern Australia.

7.8 Implications for conservation and management

The present research suggests that stocks of *T. australiensis* in south-eastern Australia are probably under exploited. For example, abundances increased throughout the study period across all sampling sites and fewer than 4% of stocks per annum are estimated to be harvested at these locations. Whilst, exploitation ratios calculated from stock assessment procedures indicated that populations in some locations, may have already reached, or are approaching optimal harvesting rates, these estimates cannot be used as a justification for restrictive management, given questions relating to accuracy of the ELEFAN procedure.

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In NSW, management of fisheries resources has undergone legislative change in recent years, with an increased emphasis on environmental sustainability (Anon, 2004b). This approach requires the development of an Environmental Impact Statement (EIS) under a proposed Fishery Management Strategy (FMS), for each

of the major commercial fisheries and the recreational fishery. The EIS predicts environmental (biological, social and economic) impacts of fishing on target stocks, by-catch species, habitats, broader ecosystem components, socio-economic issues, as well as impacts from other non-fishing activities. Incorporated into the FMS process are monitoring programs, trigger points for review of the strategy and annual reporting on performance, to ensure specific objectives are met. Areas where information is lacking and priorities for further research may also be identified.

The EIS/FMS process has been completed for the Estuary General Fishery (Anon, 2003), which endorses commercial hand gathering of *T. australiensis* in NSW. However, *T. australiensis* was not identified as a species of either primary or secondary importance in the fishery. As *T. australiensis* now appears to be primarily targeted by the recreational sector (Chapter 1), management of impacts on stocks and ecosystems is likely to depend on provisions of the EIS/FMS currently in preparation for the recreational fishery in NSW. Given that the EIS/FMS process relies on "best available information" to predict impacts, a lack of data on the basic biology and ecology of *T. australiensis* prior to the present study, is likely to confound assessments of environmental sustainability. In light of new information on the fisheries biology, ecology and recreational harvesting of *T. australiensis* in south-eastern Australia presented in this thesis, there are a number of management strategies that might now be considered in future revisions of the EIS/FMS process.

Bag limits

Results on patterns of abundance, estimated stock sizes and levels of harvesting from the present study, do not suggest a restrictive low-quantity bag limit is immediately required to reduce catches of *T. australiensis* in NSW. However, the case for developing a relatively large upper limit may be argued on other grounds including;

- The potential catch - if all harvesting parties took the maximum number of animals that were observed to be harvested during a single trip in the present study (i.e., 1000 animals), everyday of the year, then populations would experience significant declines in many areas. For example, the mean number of harvesting parties during summer low-tide periods at Maianbar was approximately 25. If these 25 parties took 1000 animals each, 365 days of the year, 9,125,000 individuals or 58% of the population would be removed per annum.

- Black market harvesting - since commercial harvesting has been bought-out of many estuaries in NSW, a bag limit may also prevent black market harvesting, which obviously occurs at some sites. For example, certain individuals were observed collecting over 400 individuals on subsequent days at Maianbar in the present study and anecdotal evidence on the existence of black market harvesting is strong.

Size limits

Minimum size limits are applied to a wide range of finfish and crustaceans in recreational fisheries, to ensure individuals have a chance to reproduce at least once prior to capture, which prevents growth overfishing. Implementing a size limit would be impractical and unnecessary for *T. australiensis* in NSW. Firstly, qualitative data from the present study, combined with quantitative data from previous studies (McPhee and Skilleter, 2002b), suggest anglers are already size selective. However, education on correct methods of discarding small shrimp is required in order to minimise predation from silver gulls and other birds. Shrimp are also extremely hard to accurately measure in the field, and size limits would be difficult to interpret for anglers and inspectors alike. Secondly, the present study demonstrated that the largest individuals of *T. australiensis* are the most fecund and would therefore be not be protected by size limits. Finally, sizes at maturity and growth parameters displayed geographic variation and differed between sexes, making implementation of size limits difficult.

Restrictions on collection of ovigerous females

Fisheries management strategies frequently involve restrictions on the collection of fish and invertebrates that are releasing or carrying eggs during breeding periods. Implementing restrictions on ovigerous females of *T. australiensis* is unjustified for sites sampled in the present study. Caution should also be exercised in using this strategy as a general precautionary management tool. For example, given that populations are significantly female-biased across a wide geographic range in south-eastern Australia, the majority of catches during breeding periods would comprise ovigerous females, which would then have to be discarded.

Incorrect discarding of the ovigerous females may subsequently lead to an increase in associated avian predation. Furthermore, banning the collection of gravid females may introduce selection pressure on large adult males, which could also have poor consequences for populations.

A greater awareness of ovigerous females by recreational anglers is suggested, which leaves the onus on the angler as to whether or not such individuals are kept or discarded. Certainly, whilst many anglers claimed they had already discarded ovigerous females in the present study, some indicated they had never noticed individuals carrying eggs under the abdomen. Again, any such education campaign should include information on correctly discarding ovigerous females (as with small individuals), to ensure discarded females are not simply preyed on by gulls, which frequently follow harvesting parties.

Closures

Temporary closures of fisheries during periods of reproduction and recruitment are common management strategies. For *T. australiensis*, reproduction and recruitment occur during spring, summer and autumn periods, which are also the most popular times of the year for recreational harvesting. Furthermore, the commencement of breeding is asynchronous, commencing earlier in southern locations in NSW compared to estuaries further north, making large-scale implementation of closures impractical. Furthermore, the data presented in this thesis does not warrant closure of any of the sites sampled in the study. Nevertheless, for local sites experiencing declines in abundance, closures during the above periods would best maximise reproductive success.

Arguments for closures, however, are not necessarily based on single-species approaches to management and may provide a number of benefits such as;

- Protection of ecosystems
- Experimental controls to investigate long-term ecological impacts
- Refuges for representative breeding populations

Marine protected areas (MPA's) may be used as part of a more permanent ecosystem approach to managing harvesting activities and protecting biodiversity. In NSW, only 2.4% of coastal waters are completely protected from harvesting activities (Jones, 2003), most of which is contained within two marine parks (i.e., Jervis Bay Marine Park and Solitary Islands Marine Park). Moreover, protection of the intertidal zone through Intertidal Protected Areas (IPA's) has largely focused on rocky shore ecosystems. Estuarine sand/mud flats are only protected in two locations in NSW; a marine sanctuary at Towra Point in Botany Bay and at Currumbene Creek in the Jervis Bay Marine Park (Anon, 2004d). Selection of MPA's has traditionally overlooked biodiversity and has often been conducted in an *ad-hoc* manner in NSW (McNeill, 1994). Consideration of sandflat areas for protection in marine reserves should recognise the fact that at many locations, harvesting of *T. australiensis* has been sustained for more than 50 years. Therefore, impacts on populations and communities may already be significant and irreversible, and conditions not representative of the habitat. For example, human disturbance in many estuaries in NSW has increased sedimentation and eroded seagrass beds (Meehan, 2001). Populations of *T. australiensis* and other macro- and meiofauna now occurring in these seagrass-denuded flats may

represent ecological succession, where anthropogenic impacts have provided ideal conditions for settlement of larvae.

Experimental closures of areas may allow long-term sustainability of harvesting on populations and wider ecosystem components to be investigated. This may only involve closure of one or two additional sites in NSW to provide adequate replication for experiments, as two closed areas currently exist in NSW (see above). This approach would be more ethical and practical compared with experiments that remove large numbers of *T. australiensis* from within sandflats, and then measure effects on populations and communities. However, experimental closures of additional areas may be politically unachievable given the focus on providing increased opportunities to the recreational fishing sector in NSW.

7.9 Conclusion

The present research has provided new baseline information on the fisheries biology, ecology and harvesting of *T. australiensis* over a range of spatial and temporal scales in south-eastern Australia. This data now provides a context in which hypotheses explaining observed patterns can be tested, using manipulative experimental approaches. Specific directions for further research have been outlined (see above). However, addressing these questions will continue to present challenges for researchers.

The immediate implementation of restrictive management is not scientifically justified for *T. australiensis* in NSW, based on results of the present research. However, further monitoring is suggested given the likelihood of an increased

demand for bait organisms associated with sustained population growth in and around urban centres, as well as continuing reallocation of fisheries resources to the recreational sector. Furthermore, questions of long-term impacts on other ecological communities and habitats remain unknown. Addressing concerns relating to the ecological sustainability of activities associated with collection of *T. australiensis* for bait, will ultimately depend on experimental investigations incorporating ecosystem approaches to management and conservation, such as marine protected areas and reserves.

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APPENDIX 1: Tagging manuscript

Preliminary evaluation of visible implant tags on the burrowing ghost shrimp, *Trypaea australiensis* in aquaria and in situ.

ABSTRACT

The utility of visible implant fluorescent elastomer (VIE) and visible implant alphanumeric (ViAlpha) tags were assessed on the burrowing ghost shrimp, *Trypaea australiensis* DANA (Decapoda: Thalassinidea: Callianassidae) in aquaria and in field based tag-recapture experiments. After 71 days in aquaria, overall mortality of individuals containing the two tag types was not significantly different from untagged controls. Retention of tags was excellent, with only one ViAlpha tag lost during the study. Although not significant, VIE tags tended to migrate within the body of *T. australiensis* more than ViAlpha tags. Recapture rates from VIE tagged individuals at liberty were low even after a period of only 3 hours, with no tagged individuals captured after a period of approximately 24 hours. The significance of the results are discussed in terms of the advantages and disadvantages of each tagging method for different applications, along with directions for future research.

INTRODUCTION

Marking or tagging techniques are commonly used to estimate age and growth of economically important decapod crustaceans, given the lack of permanent hard structures often found in other taxa. Tagging experiments conducted in aquaria and in situ can provide data on moult increment, moult frequency as well as patterns of movement for a wide range of decapods. Conventional external tags are often unsuitable for use on smaller fishes and invertebrates, leading to the development of a number of internal implant tags, including the coded wire tag (CWT), passive integrated transponder tag (PIT) and visible implant tag (Hastein *et al.*, 2001).

Northwest Marine Technology manufacture two types of visible implant tags, including the visible implant fluorescent elastomer (VIE) and the visible implant alphanumeric (ViAlpha). Marking with VIE tags involves injecting a biocompatible fluorescent liquid elastomer into suitable transparent tissue within an organism. The elastomer solidifies allowing tagging and identification of large numbers of fish or invertebrates. Unique codes can be given to particular individuals using a combination of different tagging locations and elastomer colours. ViAlpha tags are small (1.0 x 2.5 mm) alphanumerically coded polyester tags, which are also injected into transparent regions, allowing specific identification of all individuals, without the need for multiple tagging locations. The utility of both tags has been proven for many fishes (Halls and Azim, 1998; Rikardsen, 2000; Olsen and Vollestad, 2001; Griffiths, 2002; Goldsmith *et al.*,

2003) and a number of crustaceans (Godin *et al.*, 1996; Linnane and Mercer, 1998; Jerry *et al.*, 2001; Brown *et al.*, 2003).

Burrowing thalassinid ghost shrimp (Decapoda) inhabit soft substrata of coastal and marine environments across most continents (Dworschak, 2000), with the collection of several intertidal species forming significant bait fisheries in many parts of the world (Hailstone and Stephenson, 1961; Wynberg and Branch, 1991, 1994; Pezzuto, 1998; Souza and Borzone, 2003). Few studies have considered age and growth of these organisms and evidently it appears none has attempted any form of tagging. Consequently, growth parameters of thalassinid shrimp are often derived from length frequency analyses using procedures such as ELEFAN (Dworschak, 1988; Pezzuto, 1998; Souza *et al.*, 1998). The subterranean existence of ghost shrimp makes standard external methods unsuitable, possibly by restricting burrowing activity, which is also linked to the feeding mode of many species (Griffis and Suchanek, 1991). The fragility of thalassinids further confounds the use of external tags, making them ideal candidates for assessment of internal methods such as VIE and Vialpha. The present study examined the utility of VIE and ViAlpha tags in aquaria and in situ on a common eastern Australian species, *Trypaea australiensis*.

METHODS

Experiment 1: *Tagging in aquaria*

Individuals of *Trypaea australiensis* were collected from Maianbar in Port Hacking (34º05'S 151º09'E) using a manual suction pump (see Rotherham and West, 2003) for description of method). Prior to tagging, shrimp were placed into an ice bath until immobilised (~30 seconds) and then measured for carapace length (CL, mm) using digital vernier callipers. VIE and ViAlpha tags were implanted into the ventral surface of the third abdominal segment of each individual shrimp. This location was chosen in order to minimise irritation to cerebral, reproductive and/or digestive organs. This location also ensured the tag would not be covered with eggs which are carried under the 1st and 2nd abdominal segments by females. Fluorescent green elastomer was mixed and prepared according to the directions of Northwest Marine Technology, and injected into the tagging location using a 0.3 cc syringe. ViAlpha tags were implanted using the supplied needle applicator. A total of 50 shrimp were tagged, which included 25 of each tag type as well as 25 untagged controls.

Following tagging, individuals were placed in a holding tank before being randomly allocated to 5 experimental aquaria. Each aquaria consisted of a 74 L cylindrical plastic tank, filled to 1/3 of its depth with sediment collected from Maianbar (Port Hacking, NSW) (approximately 25 - 30cm) and 2/3 (40 - 50 cm) with water. Seawater was collected from a local marine dominated estuary and salinity ranged from 28 - 32 part per thousand (ppt). Water and sediment were

replaced/exchanged at the rate of one bucket per week and each tank contained a small air stone. Five individuals of each tag type were placed in each replicate aquaria, along with five control animals which had not been tagged, were still immobilized in the ice bath and measured. Each replicate aquaria therefore contained 15 individuals. Size ranges of tagged individuals were similar for each type (Table 1), ensuring mortality and tag retention was not influenced by animal size.

All individuals were removed from each aquaria 12 hours after tagging and again after 24 hours and 48 hours respectively. Shrimp were assessed for mortality, tag shedding and/or migration. It soon became apparent that the process of removing animals from the aquaria, by gently scooping through the sediment with one's hand, was traumatic for the shrimp given investment in excavating and maintaining burrows. To ensure longer survival, shrimp were checked and measured only on a further 4 occasions (6, 16, 51 and 71 days after tagging) throughout the duration of the experiment. Aquaria were checked for dead shrimp on the sediment surface every 12 - 24 hours. It was originally intended to run the experiment for a 10-week period as previous studies (unpublished data) indicated that it was difficult to maintain shrimp for longer periods. In fact, the experiment was concluded after 10 weeks due to high mortality levels of shrimp.

One-way ANOVA was used to test for differences in overall mortality between tag types (VIE, ViAlpha, control). Data were tested for normality and homogeneity of variances using Shapiro-Wilk and modified Levene's tests respectively and no transformation was necessary.

Experiment 2: *Tagging in situ*

Experiments were carried out during low-tide on an intertidal sandflat at Maianbar, Port Hacking between 30th April 2003 and 2nd May 2003. A 10 m x 10 m plot was haphazardly chosen and within this plot, 5 replicate 1 m x 1 m quadrats were randomly selected and pegged out using wooden stakes, which protruded approximately 4 inches out of the sediment. Fluorescent stringline was used to fence and delineate the quadrats. *T. australiensis* were collected from other areas of the sandflat and 100 individuals immediately tagged with VIE tags. Twenty individuals were then placed into each quadrat and allowed to burrow, by either saturating the surface with water, or placing animals into finger holes and covering with sediment. Prior to the quadrats being covered by the flood tide (approx 2 hours), 100 pumps of the yabby pump (4 pumps at 25 points) were done in each quadrat, effectively saturating the area. Contents of the pump were sieved over coarse plastic mesh (10 mm) and numbers of tagged and untagged individuals recorded. The same process was undertaken in a second 10 m x 10 m area on 1st May 2003. However on this occasion, harvesting of the five 1 m x 1 m quadrats was left until low-tide the following day (approx 24 hours), effectively allowing completion of another 2 tidal cycles. Tag/recapture experiments enable stock sizes (N) to be estimated using the Peterson method: $N = TC/R$, where T = number of tagged fish, C = total catch and R = recaptured tagged fish. Standard errors are calculated according to the equation $se = \sqrt{[T^2C\ (C\text{-}R)\ /\ R^3]}$ (King, 1995). Population densities were estimated within the 1 m x 1 m quadrats using this method.

RESULTS

Tagging *Trypaea australiensis* with ViAlpha tags proved more tedious than with VIE, as a new tag had to be loaded into the applicator for each animal. The VIE filled syringe enabled rapid tagging of individuals and the small needle resulted in more accurate placement of tags. Both types of tag were easily identified with the naked eye, although an ultraviolet light was often needed to find tags that had moved from the original tagging location in the third abdominal segment. Tag migration (mean %) within animals was not significantly different between tag types (*t*-test, $P > 0.05$), although a trend of increased movement of VIE tags was evident (Fig. 1). Despite the mobility of both types of tags within animals, only one individual lost or "shed" a tag, which was a ViAlpha type.

On completion of the experiment after 71 days, mean mortality of *T. australiensis* was greater than 95% across all tag types (Fig.2). ANOVA revealed no significant difference in the overall mean mortality rates between tags ($F = 0.27$, $P > 0.05$). Despite no significant differences between tagging methods, a trend of lower mortality in VIE tagged animals compared to control and ViAlpha individuals was evident throughout most of the study (Fig. 2). Measurement of the only remaining ViAlpha tagged individual indicated growth was 0.8 mm over the 10 week period.

In field tagging experiment, the number of recaptured *T. australiensis* from each of the five 1 m x 1 m quadrats during the same low-tide period, ranged from 1 - 6 individuals (5 – 30%) (Table 2), with a mean of 3 (±1) animals or 15 (±5.24) %.

Population densities within plots, estimated using the Peterson method ranged from 67 (±5) to 600 (±589) individuals (Table 2). For quadrats that were sampled at low-tide on the following day, no tagged animals were recaptured.

DISCUSSION

The present study although preliminary in nature, has shown both VIE and ViAlpha tags to be effective at marking individuals of *Trypaea australiensis*, from sub-adults through to adults (Table 1). In fact, mortality rates of untagged control individuals were not significantly different from tagged individuals (Fig. 1). Tag retention was also high, with only one ViAlpha tag lost during the study. While the use of either method may depend on the type of study being conducted, it is clear that VIE tags may be suited a wider range of applications. For example, VIE tags are particular effective at marking large numbers or cohorts of shrimp, given the ease and accuracy at which tags can be placed. This makes VIE tags particularly amenable to field tagging programs studying growth, movement or population densities. ViAlpha tags would not be especially suitable for field investigations requiring large numbers of shrimp to be tagged, as implanting the tag requires far more skill and concentration, given the larger size of the needle relative to the syringe used for VIE tags. Furthermore, the applicator must be reloaded with a new tag for each individual, which can be time consuming.

Advantages of ViAlpha tags most likely lie in experimental aquaria, where growth rates of specific individuals can be measured. However, the larger size of ViAlpha

tags compared to VIE tags, which can made be as small as desired, probably limits the application on small on juvenile shrimp (e.g. 5mm, CL). Unique marks can be created using combinations of different coloured elastomer and tagging locations. Only one tagging location was assessed in the present study and clearly, there is much scope for assessing alternative sites such as the carapace, eyestalks and other abdominal segments. The tendency for VIE tags to migrate throughout the body of *T. australiensis* (Fig. 2), perhaps a result of their smaller size, shows that other tagging locations may be possible and are unlikely to affect survival.

The difficultly in keeping *T. australiensis* alive in aquaria limits many aspects of controlled tagging experiments. Burrowing activity has been linked to trophic modes for this species, which is a deposit feeder that collects organic matter whilst constructing and maintaining burrows (Kenway, 1981; Boon *et al.*, 1997). Substituting diets with shredded algae (*Enteromorpha* spp.) and brine shrimp proved unsuccessful (unpublished data) in the present study. Replacing sediment was the only way to maintain shrimp for long periods. However, the constant disruption of this process seemed to result in higher mortality, possibly due to the fragility of the organism. Dworschak (1988) reported keeping individuals of *Callianassa tyrrhena* alive in aquaria for up to three years. Application of VIE and ViAlpha tagging methods on to this and indeed other such species is encouraged.

The field experiment found small numbers of individuals could be recovered from 1 m x 1 m plots within a period of 2 hours (Table 2). Density estimates from the recapture experiment were higher than ranges obtained from extrapolating CPUE

data for the same location (Rotherham and West, in prep). Given the small time frames and exhaustive sampling method, more recaptures of tagged individuals were expected. This supports an hypothesis that *T. australiensis* are highly mobile (Rotherham and West, in prep), choosing either to leave quadrats in search of vacant burrows and space, or being forced out through agonistic encounters with other shrimp (Hailstone, 1962; Tunberg, 1986; Felder and Lovett, 1989; Rowden and Jones, 1994; Labadie and Palmer, 1996). Certainly, no shrimp burrowed back up to the surface of the sediment. A logical extension of this experiment would be to denude 1m x 1m plots containing *T. australiensis* prior to restocking with tagged individuals, to reduce competitive interactions. The fact that no tagged individuals were recaptured from plots containing shrimp that had been at liberty for 24 hours, indicates that future experimental studies may need to tag very large numbers of shrimp, possibly as many as 100 m^2 in order to get adequate returns. This may restrict wider application of tagging techniques to larger scale experimental field studies or monitoring programs, which ultimately rely on the recapture of tagged individuals.

Table 1. Number, length range (mm) and mean length (±SE) of *T. australiensis* tagged with visible implant elastomer (VIE) and visible implant alphanumeric tags (ViAlpha). Controls represent individuals that were untagged but also underwent immobilization in ice-baths.

Tag type	Number tagged	Length range (mm)	Mean length (mm)
ViAlpha	25	8.15-12.150	10.03 (0.25)
VIE	25	8.29-13.140	10.53 (0.28)
Control	25	7.37-11.210	9.69 (0.20)

Table 2. Number of tagged and untagged individuals recaptured from five 1 m x 1 m quadrats containing 20 *T. australiensis* tagged with visible implant elastomer (VIE) tags. Quadrats were harvested approximately 3 hours after liberty of animals. Stock size and standard error (±SE) refers to estimated density within each individual quadrat calculated using the Peterson method (see text for details and King, 1995).

Quadrat	Tagged	Untagged	Stock Size *N*	SE
1	6	14	66.66	5.09
2	2	22	240	162.48
3	5	13	72	27.36
4	1	26	540	529.91
5	1	29	600	589.91

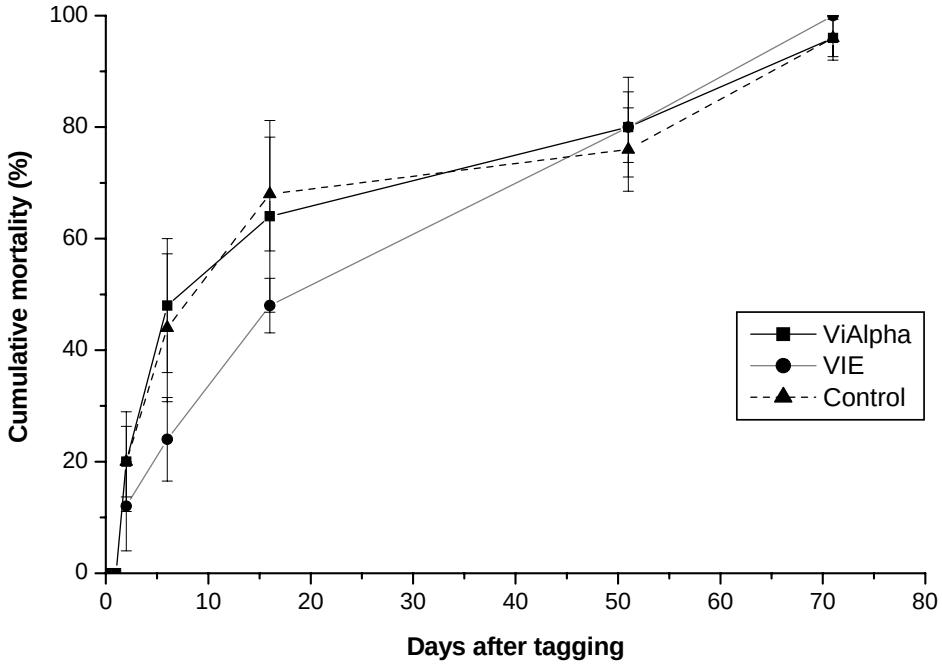

Figure 1. Percentage cumulative mortality (±SE) of *T. australiensis* in aquaria over a 71 day period following tagging with visible implant fluorescent elastomer (VIE), visible implant alphanumeric (ViAlpha), compared to control (untagged) individuals.

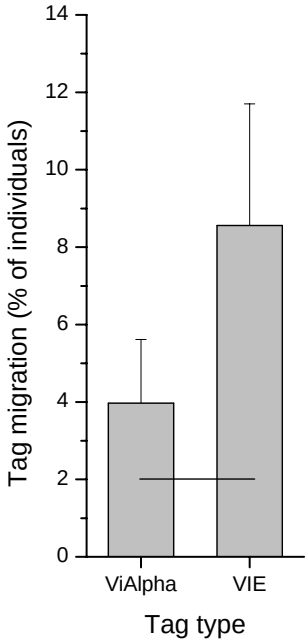

Figure 2. Mean percentage (±SE) of tagged *T. australiensis* individuals in which visible implant fluorescent elastomer (VIE) and visible implant alphanumeric tags (ViAlpha) migrated out of the original tagging location during a 10-week experiment in aquaria. Horizontal line joins means with no sigificant difference (*t*-test, $P > 0.05$).

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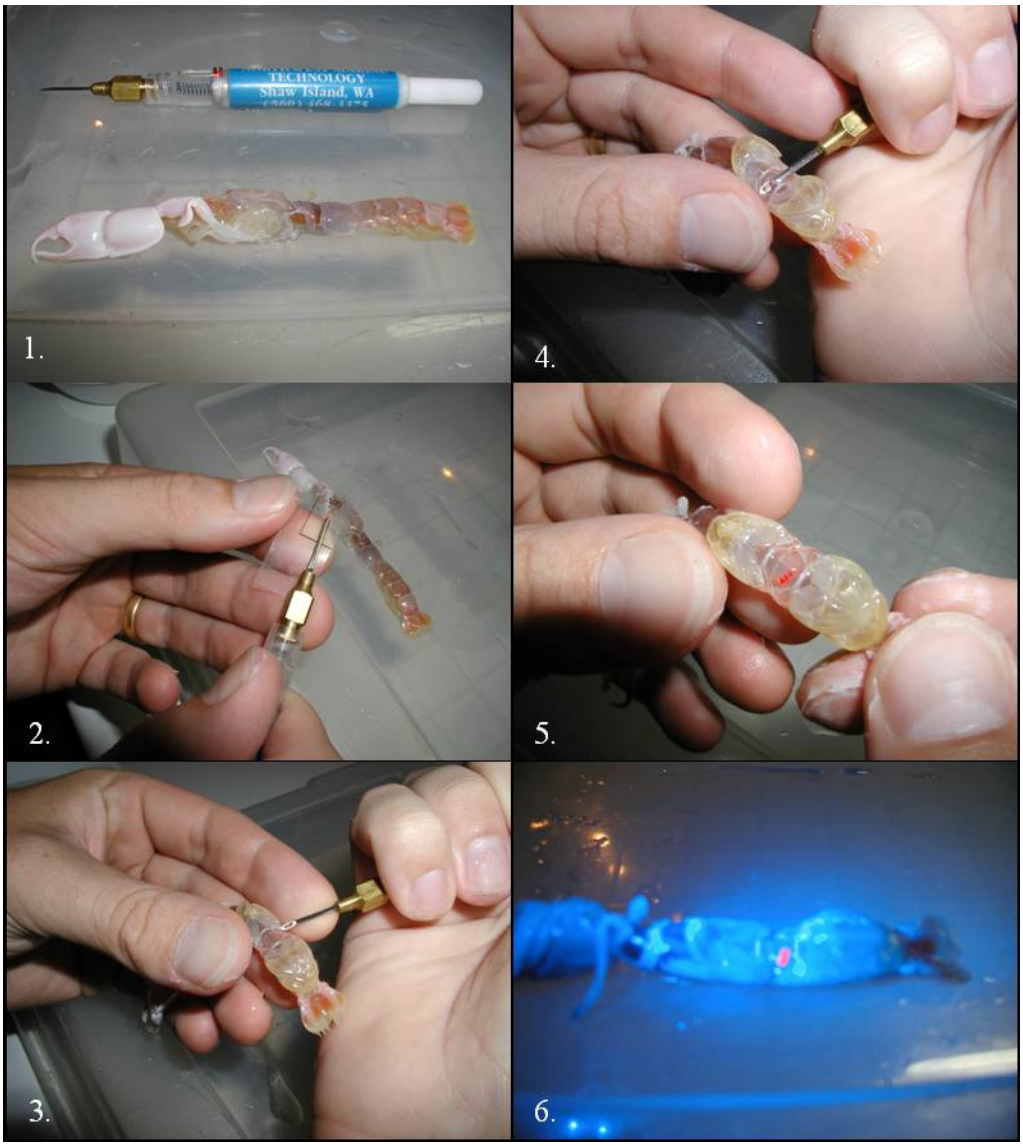
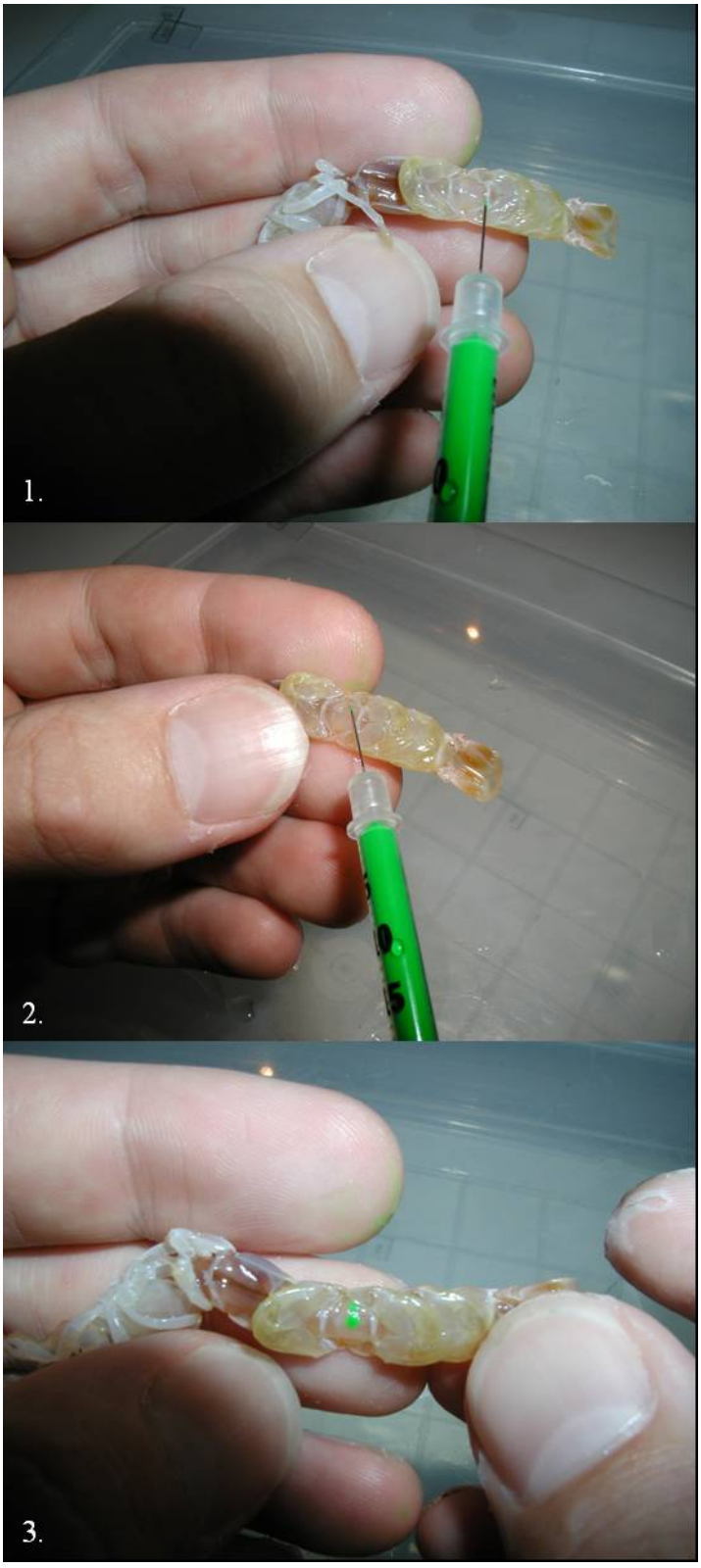
APPENDIX 2: Photographs of tagging processes



Tagging a male individual of *T. australiensis* with a ViAlpha tag and illumination of tag under ultraviolet light.



Tagging a male individual of *T. australiensis* with a VIE (Visual Implant Elastomer) tag.

APPENDIX 3: Photographs of study sampling sites

Maianbar, Port Hacking: Looking towards the entrance in an easterly direction during an outgoing tide (photo not representative of entire sampling area).

Cabbage Tree Basin, Port Hacking: Looking in a southerly direction during an outgoing tide. (photo not representative of entire sampling area).

Shoalhaven Heads, Shoalhaven River: View of sampling site at low-tide looking in a south-westerly direction. (photo not representative of entire sampling area).

Old Man Island, Shoalhaven River. Looking in a north-westerly direction at low-tide. (photo not representative of entire sampling area).

Garlandtown, Moruya River: Looking in a south-easterly direction at low-tide. (photo not representative of entire sampling area).

Quondolo Island, Moruya River: Looking in a westerly direction at low-tide (photo not representative of entire sampling area).